MEMOIRS

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OLIGOCENE CANIDÆ.

By J. B. Hatcher.

While collecting in the Oligocene deposits in the Hat Creek Basin, Sioux Co., Nebraska, during the season of 1901, Mr. O. A. Peterson was fortunate in discovering an almost complete skeleton (No. 492) of an extinct dog, which I have referred to the species recently described by Prof. W. B. Scott as *Daphænus felinus*, although it differs in certain skeletal and dental characters which by some might be considered as of specific importance.

In about the same geological horizon and in the same general locality (Hat Creek Basin) Mr. Peterson also discovered portions of the skeletons of three other dogs. All of these have the skull for the most part well preserved. One of these (No. 553) pertains to *D. felinus*, while a second (No. 491), I have been unable to identify with any known genus or species. The third (No. 552), which consists of a remarkably complete skull with lower jaw, atlas, axis, third cervical, and other portions of the skeleton, while generically agreeing very well with Cope's description of *D. hartshornianus*, presents such striking differences from those given by Leidy for *D. vetus*, the type of the genus, that I have thought it best to erect for this also a distinct genus and species.

By reason of the remarkably perfect condition of this material, and more especially of the skeleton of *Daphænus felinus*, which for the first time makes it possible to determine the more important osteological and dental characters of that genus from a single skeleton, I have thought it desirable to figure and describe this material in detail. Notwithstanding the recent contributions by Scott, Wortman, and Matthew to our knowledge of the Oligocene canidæ it is believed that a careful

study of this recently acquired material will add something to our knowledge of the osteology of *Daphænus* and may perhaps shed some new light on the phylogenetic relations of this genus to the modern carnivora and more especially to the modern canidæ.

Generic Characters of Daphœnus[1] Leidy.

Proc. Acad. Nat. Sci., Phila., 1853, p. 393. *Amphicyon* Leidy (non Lartet), ibid., 1854, p. 157; Ext. Mamm. Fauna Dak. & Nebr., 1869, pp. 32, 356; Cope, Tertiary Vertebrata, pp. 894, 896. *Canis* Cope, Ann. Report U. S. G. S. of the Terrs., 1873, p. 505. *Daphænus* Scott, Trans. Am. Phil. Soc., Vol. XIX, pp. 325 415; Wortman and Matthew, Bull. Am. Mus. Nat. Hist., Vol. XII, pp. 100-138.

The type species of this genus is *D. rctus*, founded by Leidy on "a cranium without the face, a fragment of a left maxilla containing the posterior three molars, the posterior portion of the left side of the lower jaw containing the last two molars, and a lower ante-penultimate molar of the left side."

Leidy's original description of this genus and species is as follows: "The cranium is elongated and narrow and possesses very much the form of that of the recent *Paradoxurus*. The glenoid articulation is transversely concave as in the weasels, etc. The auditory bullæ are comparatively small. Of the superior posterior three molars, the last is the smallest, and has a simple oval crown; the penultimate is second in size and resembles that of the wolf, but is broader in relation to its antero-posterior diameter; and the ante-penultimate is the largest, and also resembles that of the wolf, but is more trilateral, relatively broader compared with its antero-posterior diameter, and has less elevated tubercles.

"Of the inferior posterior three molars, the last is smallest and very like that of the wolf; the penultimate is next in size, and has an oval crown as in the wolf, but has much less elevated tubercles; and the ante-penultimate which is the longest, in relation to the size of the animal, is much smaller than in the wolf, but it has the same general form; presenting a broad heel behind, worn off flat in the specimen, and three lobes anteriorly, having the same relation to one another, as in the wolf, but more nearly equal in size and forming together more of a triangle."

This brief description is followed by a few measurements of the different elements constituting the type specimens. In the following year[2] Leidy considered his genus *Daphænus* as a synonym of *Amphicyon* which had previously been proposed by Lartet[3] for the reception of certain remains of canidæ found in the Mio-

[1] Leidy's original spelling of this word was *Daphœnus*, not *Daphænus* as spelled by more recent writers. Since the former is, moreover, the correct latinized form of the Greek *daphoinos*, it has been thought best to retain the original form.

[2] See Proc. Acad. Nat. Sci. Phila., 1854, p. 157.

[3] See Bull. Soc. Geol., 1836, VII., p. 219.

cene formation at Sansans, France. The reference of this material to the genus *Amphicyon* seems to have been based entirely upon the dental formula and is now known to be erroneous, as has been shown by Scott. The chief generic distinctions between *Daphænus* Leidy and *Amphicyon* Lartet in so far as they are at present known are to be found in the relative size of the premolars, structure of canines, and position of the superior third tubercular molar. The canines of *Daphænus* are without either anterior or posterior cutting edges, while these are present in *Amphicyon*. The premolars are reduced in size in *Amphicyon*, while those of *Daphænus* show little or no reduction. In *Daphænus* the superior third tubercular molar is pushed inward and aligned with the internal cones of the preceding molars, while in *Amphicyon* this tooth occupies a more external position.

In 1869,[4] as *Amphicyon vetus*, Leidy gave a much more complete description of the material which had formed the type of his previously proposed genus *Daphœnus*. Among the more important additional characters then enumerated by him the following may be mentioned as being perhaps of generic importance.

1. Presence of long, strong and high sagittal crest.
2. Auditory bullæ small.
3. $M.^3$ small, transversely oval, with two tubercles and one root.

In 1898[5] Scott confirmed most of the observations made by Leidy and added a great number of new characters relating not only to the skull and dentition, but to other portions of the skeleton as well. In this paper Professor Scott gave the first adequate account of the osteology of the genus *Daphænus* and pointed out its distinction from *Amphicyon*. On account of the incomplete nature of the material at his command Scott's description was necessarily based on the remains of several more or less fragmentary skeletons belonging to different species. Moreover, as we shall show later, it is not at all certain that some of the material described by Scott does not pertain to a distinct genus.

In 1899 Wortman and Matthew[6] characterized the genus *Daphænus* Leidy as follows: "Upper molars transversely unsymmetrical (paracone more external than metacone). M^3 oval, aligned with inner cusps of anterior molars. Heels of lower molars low-ridged, with low entoconid crest, $m_{\overline{3}}$ a convex nub."

Combining the characters above noted with those shown by the material under discussion, the genus *Daphænus* may be distinguished by the following cranial and dental characters.

[4] See Journ. Acad. Sci. of Phila., 1869, pp. 31–36.

[5] See Trans. Am. Phil. Soc., Vol. XIX., pp. 325–415.

[6] See Bull. Am. Mus. Nat. Hist., Vol. XII., p. 129.

Dentition $I\frac{3}{3}$, $C\frac{1}{1}$, $P\frac{4}{4}$, $M\frac{3}{3}$; *premolars but little or not at all reduced in size; anterior premolars separated by considerable diastemata; canines stout and without anterior or posterior cutting edge; sagittal crest long and very high throughout its entire length, extending a little in front of temporal constriction; capacity of brain-case very small in proportion to size of skull. Rami of lower jaw not coössified, with inferior border very sinuous and symphysial area much restricted.*

DAPHŒNUS FELINUS Scott.

Specific characters: Scott has distinguished this species as follows:

"The inferior dental series of this species slightly exceeds in length that of *D. vetus* and the sectorial is larger. The lower tubercular molars are inserted in the border of the ascending ramus of the mandible, and, judging from the alveoli, were reduced in size. The horizontal ramus is not much longer, but much heavier than in *D. vetus*, and has a more sinuous ventral border, which rises more beneath the masseteric fossa. The limb bones and vertebræ are somewhat larger and heavier than in *D. vetus*, and the neural spines of the lumbar vertebræ are very high and inclined strongly forward. In size *D. felinus* is the largest and most massive species of the genus."

Among the material in our collections secured by Mr. Peterson are portions of two skeletons, Nos. 492 and 553, which I have referred to this species, although they do not in all respects agree with the characters mentioned above. This is especially applicable to the position of the lower tubercular molars, which in *D. felinus*, according to Scott, are inserted in the border of the ascending ramus. In No. 492 both rami are well preserved, and one of these teeth is still in situ, but its position is in the horizontal ramus rather than the ascending, as is well shown in Pl. XVI., Fig. 2. I do not, however, consider this difference as of specific importance, since, on actual comparison, our material, in other respects, agrees remarkably well with the type. While belonging to a slightly smaller individual it is decidedly larger than the type of *D. vetus*, and differs from the latter in a number of important characters.

THE DENTAL AND OSTEOLOGICAL CHARACTERS OF DAPHŒNUS FELINUS Scott.

The following description of the dental and osteological characters of *D. felinus* is based on the following material, belonging to the collections of this Museum.

No. 492, consisting of a nearly complete skull with lower jaw, atlas, 12 dorsals,

6 lumbars, 15 caudals, 5 sternals, a nearly complete set of ribs, left humerus, radius, ulna and pyramidal, right humerus, radius, ulna and manus except the pyramidal, both hind limbs and feet, and the patellæ and os penis.

No. 553, consisting of a skull without the lower jaw, much injured posteriorly on the right side, with P. $\frac{2}{}$, $\frac{3}{}$, $\frac{4}{}$ and M. $\frac{1}{}$, $\frac{2}{}$ in excellent preservation. Associated with this skull there were found a calcaneum, two caudals, and a few other fragments. Both specimens are from the Oreodon beds on Bad Land Creek, Sioux Co., Neb. Unless otherwise stated the following description will be based on No. 492.

The Skull, Pl. XIV., Figs. 1 and 3, Pl. XVI., Fig. 5.

Seen from the side the skull of *D. felinus* is low, with the facial region much abbreviated and the fronto-parietal region somewhat elongated. The distance from the anterior margin of the orbits to the extreme front of the premaxillaries is only about one third the total length of the skull.

Viewed from above the brain-case appears narrow and the zygomata widely expanded. The maximum temporal constriction is a little in advance of the point where the superciliary ridges unite to form the high sagittal crest. The fronto-maxillary region is broad but converges rapidly in front. There is a slight constriction posterior to the canines.

The premaxillaries are small, with rather deep external lateral grooves for the reception of the inferior canines. The incisive alveolar border is placed nearly at right angles to the longer axis of the skull. Posteriorly the premaxillaries send back slender processes which are intruded between the anterior portions of the maxillaries and nasals, but are widely separated by those bones from the anterior projection of the frontals.

The nasals are rather broad anteriorly but narrowed posteriorly. They are extended far back between the frontals.

The maxillaries are very broad posteriorly but narrow anteriorly. They are in contact with the nasals throughout about one half the length of the latter. They are excluded from the anterior border of the orbits by the malars and lachrymals. Inferiorly the maxillo-premaxillary suture bisects the alveolus of the canine. The infraorbital foramen is large and is situated immediately above the anterior portion of the superior sectorial and the posterior portion of P.^{3}. The maxillaries are continued posteriorly to form the floor of the orbits and give support to the superior molars.

The malar forms much the larger portion of the anterior and inferior border of the orbits and sends backward a rather long process which unites, by an extended

suture, with the zygomatic process of the squamosal to form the rather slender, but widely expanded, zygomatic arch.[7]

On account of the old age of both the animals to which our skulls belonged it is impossible to determine the exact character of the lachrymals. They are seen, however, to form a very small portion of the anterior border of the orbits.

The frontals are broad and convex transversely, indicating the presence of quite capacious frontal sinuses. Anteriorly they are separated for a considerable portion of their length by the nasals. Posteriorly and superiorly they display rather rugose superciliary ridges. These converge quite rapidly and unite to form the extremely

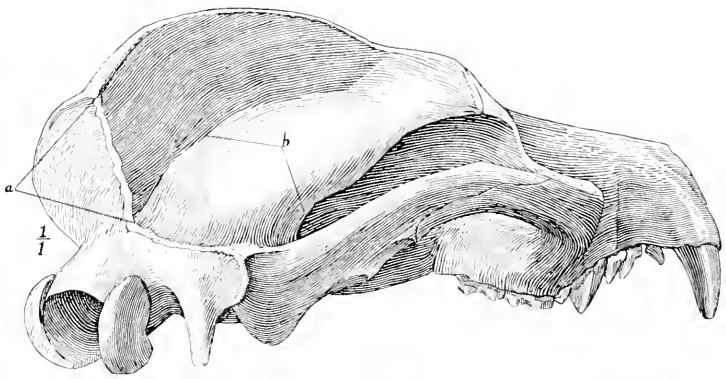


Fig 1. Skull of *Daphœnus felinus* Scott, with occipital crest removed from right side to show the great development of sagittal and occipital crests; *a*, superior and inferior limits of sagittal and occipital crests; *b*, superior and inferior borders of brain-case. Natural size but foreshortened. (No. 492.)

high and sharp sagittal crest, which is more prominent than in any recent carnivore known to the present writer.

The sutures of the cranial region are so obliterated by age in both individuals that it is impossible to determine the relations of the different elements of this region. Posteriorly the sagittal crest expands into an extremely high and sharp occipital crest which overhangs the occipital condyles. By this unusual development of the sagittal and occipital crests the capacity of the brain-case is reduced to a minimum. The relative development of these crests as compared with the capacity of the brain-case in *Daphœnus* is comparable only with that which obtains in Didelphys among recent mammals or in some of the Oligocene Elotheres and Hyænodons.

[7] The zygomatic arches in Daphœnus have been generally described as robust, but they are well preserved in the present specimens and I find them more slender than in modern canines of equal size.

This extraordinary development of the sagittal crest at the expense of the capacity of the brain-case in *Daphænus* will perhaps prove to be the most distinctive character of the genus. It is well shown in Pl. XIV., Fig. 2, and in Fig. 1 of the text.

The condyles are not entirely complete in either skull. They appear to have been subelliptical in outline with the vertical diameter the longer.

The foramen magnum has the transverse diameter exceeding the vertical, a character which from the material at my command seems to be remarkably constant with the thoöid members of the canidæ, while in the alopecoid series the reverse seems to be the case.

The zygomatic process of the squamosal extends abruptly from the side of the skull nearly at right angles to the longer diameter of the latter, then bends forward and upward so as to overlap the zygomatic process of the malar.

The temporal constriction is very pronounced and the transverse diameter of the cranium at this point is only a little more than one fourth the greatest expanse of the zygomata and one half that of the cranium proper at its widest point between the zygomatic processes of the squamosals.

The palate is broad posteriorly, but narrow in front, and slightly constricted between P. $\frac{1}{1}\frac{\&}{\&}\frac{2}{2}$. Owing to age the sutures between the palatines and maxillaries are not very distinct. The latter bones appear however to form a more considerable portion of the surface of the palate than do the former, while the extreme anterior portion is formed by the premaxillaries. The anterior palatine foramen is moderately large and is enclosed by the premaxillary except postero-externally, where it is bounded by the maxillary. Owing to the imperfect nature of the specimen it is impossible to determine with accuracy the number or nature of the posterior palatine foramina. The posterior border of the posterior nares is a little behind the last tubercular molar as indicated by the alveolus of that tooth.

The pterygoids are long and curve inwards inferiorly so as to partially enclose the posterior portion of the narial orifice. The hamular processes have been broken away and the condition and age of the specimens do not permit of determining to what extent the palatines and alisphenoids respectively enter into the formation of the pterygoids.

The sutures between presphenoid, basisphenoid, and basioccipital are closed and these bones are all fused as one.

The paroccipital process is slender, styliform, and directed downward and somewhat backward. The mastoid process is low, broad, and separated from the postglenoid process by a wide and deep groove very similar to that which obtains in the modern canidæ, and it doubtless served as in the latter to accommodate the tubular

process of the auditory bulla which enclosed the *external auditory meatus*. The postglenoid process curves slightly forward and overhangs somewhat the glenoid cavity, though not to so great an extent as in the modern wolves. The character of this process is intermediate between that of the modern cats and dogs. The anterior border of the glenoid cavity is flat as in the dogs rather than depressed as in the cats, so that the articulation of the lower jaw is dog-like in nature rather than feline.

Leidy and Scott have both described the auditory bulla of *Daphœnus* as being exceedingly small, though both express some doubt as to the homology of the elements which they have described as auditory bullæ. The following quotation from Scott sets forth the chief characters as described by each of these authors. He says: "The auditory bulla of *Daphœnus* is very remarkable and differs from that of any other known carnivore. Its principal characters were observed and noted by Leidy, but the material at his command was insufficient to enable him to describe these peculiarities with confidence. The *tympanic* is exceedingly small and is but slightly inflated into an inconspicuous bulla, the anterior third of which is quite flat and narrows forward to a point. There is no tubular auditory meatus, the external opening into the bulla being a mere hole, but the anterior lip of this opening is drawn out into a short process, somewhat as in existing dogs. Behind the bulla is a large reniform vacuity or fossa of which Leidy remarks: 'At first, it appeared to me as if this fossa had been enclosed with an auditory bulla and what I have described as the latter was a peculiarly modified auditory process.' Several specimens representing both the White River and John Day species of *Daphœnus* show that the fossa is normal and was either not enclosed in bone, or, what seems less probable, that the bony capsule was so loosely attached that it invariably became separated from the skull on fossilization, . . ."

After a careful examination of our material and after comparing it closely with the skulls of recent dogs, I am convinced that those elements which have been described by Leidy and Scott as auditory bullæ are in fact that portion of the petrosal enclosing the cavity of the internal ear, while in each instance the auditory bulla has been lost, as from the above quotation it will be seen that both these authors had suspected. Not only do the backwardly projecting paroccipitals, and widely separated mastoid and postglenoid processes indicate the presence of a moderately developed if not large auditory bulla, but on the inner portion of the squamosals and external surfaces of the basiphenoid may be seen marks of the sutures by which they were once loosely attached to these bones. Moreover if we remove the auditory bulla, as may easily be done, in the skull of any recent dog so as to expose

that portion of the petrosal enclosing the cavity of the internal ear, as shown on the left side in Fig. 2, we shall find a very close similarity between that structure and that which has been described by Leidy and Scott as the auditory bulla. The minute external opening described by Scott is no doubt the *fenestra rotunda* of the petrosal and not the external opening to the auditory bulla. The reniform fossa noted by Leidy is present also on the postero-internal side of the petrosal, though not so pronounced in recent species of Canis. Not only do all these and many other characters go to show that this element is in reality the petrosal, but a fragment of the tympanic has been retained in skull No. 492 and is shown in position and overlying the petrosal in Fig. 3. A careful comparison of Figs. 2 and 3 will make it

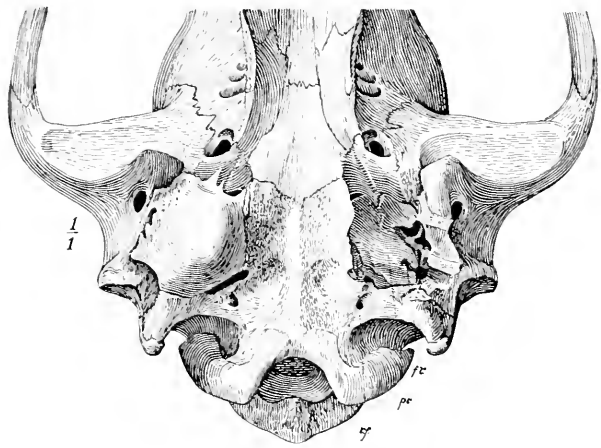


FIG. 2. Inferior view of basicranial region of skull of *Canis familiaris* with auditory bulla removed from left side to show structure of inner ear for comparison with Fig. 3; *r f.*, reniform fossa; *pr*, promotory; *f.r.*, fenestra rotunda.

apparent that the bone in question is the petrosal and that through imperfect connection with the surrounding elements the auditory bullæ have very generally been entirely lost in *Daphænus* during the process of fossilization. Considering this in connection with the fact that in several species of recent dogs, even in adults, the auditory bullæ are easily detached, this may be considered as a primitive condition among the canidæ, while the completely ossified and firmly ankylosed auditory bullæ should be regarded as more specialized characters.

The petrosal therefore is the element which has been mistaken by Leidy and Scott for the auditory bulla. It is proportionately smaller than in the modern

canidæ and in general form it resembles more nearly that which obtains in the felidæ than in the canidæ. Seen from below the general shape of the *promontory* is pyriform with the expanded end directed posteriorly and externally and the apex looking anteriorly and internally. The inferior surface of the *promontory* is convex in all directions as in the cats and not so much flattened as in the modern dogs. The *fenestra rotunda* opens downward, outward and backward, and is more canine than feline in character. The foramen or *fenestra ovalis* looks directly outward toward the groove between the post-glenoid and mastoid processes, but is situated

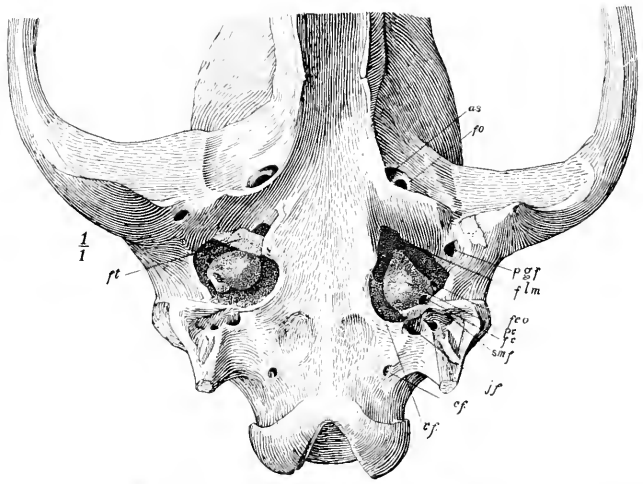


FIG. 3. Inferior view of basicranial region of skull of *Daphœnus felinus* (No. 492). *f.t.*, fragment of tympanic; *as.*, posterior opening of alisphenoid canal; *f.o.*, foramen ovale; *p.g.f.*, postglenoid foramen; *f.l.m.*, foramen lacerum medium; *fe.o.*, fenestra ovalis; *pr.*, promontory; *f.r.*, fenestra rotunda; *sm.f.*, stylomastoid foramen; *j.f.*, jugular foramen; *c f.*, condylar foramen; *r.f.*, reniform fossa.

high above the roof of that groove. The inflated nature of the *promontory* indicates that the cavity of the internal ear was capacious and the cochlea correspondingly well developed.

In neither of our skulls is the basicranial region sufficiently well preserved to determine with certainty the position or character of all the foramina of this region. In No. 492, however, the following foramina may still be detected and are shown in Fig. 3. The *condylar foramen* perforates the exoccipital at the usual place just within the base of the paroccipital process. The *foramen lacerum posterius* occupied a position on the postero-internal side of the auditory bulla. The *postglenoid fora-*

men lies at the postero-internal base of the postglenoid process. The *foramen lacerum medium* was situated at the antero-internal angle of the auditory bulla. The *foramen ovale* and posterior opening of the *alisphenoid* canal were a little less separated than in modern dogs and opened by a single rather elongate and oval aperture situated external to the posterior extremity of the pterygoid. The *alisphenoid* canal appears to have been small, but long, so that its *anterior opening*, the sphenoidal fissure and the *optic foramen* are crowded close together and all occupy a comparatively small space at the base of the pterygoids.

MEASUREMENTS (No. 492).

Greatest length of skull	205 mm.
Greatest expanse of zygomata, distortion eliminated	119 "
Length of sagittal crest	95 "
Height of sagittal crest at point of union with occipital crest	28 "
Height of sagittal crest above greatest expanse of brain-case	16 "
Length of zygoma	93 "
Breadth of cranium at point of greatest constriction	31 "
Greatest breadth of cranium	58 "
Expanse of frontals at postorbital processes	43 "

THE MANDIBLE, PL. XIV., FIG. 2; PL. XVI., FIGS. 2 AND 4.

The lower jaw is not unusually heavy for a dog of the size indicated by the skeleton. The horizontal ramus is perhaps a little deeper than in modern wolves of the same size, but no thicker. The rami are not coössified. The inferior border is very sinuous and posteriorly it is produced into a slender and hooked angular process. The coronoid process is remarkably broad, thin posteriorly and superiorly, but much thickened quite to the summit anteriorly. The condyle is situated slightly above the alveolar border. It is subcylindrical, and with the articular surface, broad internally and narrow externally. This surface looks backward rather than upward when the jaw is held in a horizontal position. The masseteric fossa is deep and broad. Anteriorly, inferiorly and posteriorly, it is bounded by prominent ridges of bone, developed on the anterior border of the ascending ramus, the postero-inferior border of the horizontal ramus, and that portion of the posterior border of the ascending ramus which gives support to the external portion of the condyle. There are two *mental foramina* situated about midway between the superior and inferior borders of the ramus. One of these, the anterior, is located directly below the anterior root of $P._{\overline{2}}$, while the posterior lies below the same root of $P._{\overline{3}}$. The *inferior dental foramen* is placed near the inferior border and midway between the angle of the ramus and the last tubercular molar.

Measurements.

Length from condyle to incisive alveolar border	152 mm.
Height of condyle above angular process	30 "
" " coronoid " " "	68 "
Width of coronoid at summit	26 "
Depth of ramus below middle of sectorial	26 "
" " ramus below $P._{\overline{1}}$	21 "

The Teeth.

The dental formula is $I.\frac{3}{3}, C.\frac{1}{1}, P.\frac{4}{4}, M.\frac{3}{3} - 44$. All the teeth are represented in our specimens and in good preservation except the incisors, $P.^{\underline{1}}$ and $_{\overline{2}}$ and $M.^{\underline{3}}$, these are shown only by the alveoli or roots in either jaw of our skulls. By mistake the superior incisors and $P.^{\underline{1}}$ were shaded in from a third skull belonging to a distinct species in the drawing reproduced in Plate XVI., Fig. 5.

Superior Dentition.—Pl. XVI., Fig. 5. The incisive alveolar border extends nearly at right angles to the longer axis of the skull. Only the roots of the incisors are preserved. These show that $I.^{\underline{1}}$ and $^{\underline{2}}$ were small, very much compressed laterally and subequal in size, while $I.^{\underline{3}}$, although small as compared with the same tooth in recent dogs, was much stronger than the two preceding teeth, a character not shown in the illustration, which is erroneous in that respect. Between $I.^{\underline{3}}$ and the canine there is in the premaxillary a deep depression into which fitted the point of the inferior canine.

The canines are blunt, stout, and without anterior or posterior serrated or cutting edges. They are fixed in the jaw by large fangs and are directed downward, forward and outward.

$P.^{\underline{1}}$ is represented only by the fang. It was fixed in the jaw by only a single root and its crown was probably not very different from that shown in the drawing. It was separated from the canine and from $P.^{\underline{2}}$ by considerable diastemata.

$P.^{\underline{2}}$ has two roots and a single median cusp. The transverse diameters of the anterior and posterior portions of the crown are subequal. Its longer diameter is parallel with that of the skull. A short diastema separates this tooth from the succeeding premolar.

The crown of $P.^{\underline{3}}$ supports a single median cusp with a low, broad heel posteriorly and a much narrower anterior portion. There is a rather well-defined basal cingulum along the internal and posterior borders of this tooth. There is no diastema between $P.^{\underline{3}}$ and the superior sectorial. At the anterior margin of $P.^{\underline{3}}$ the alveolar border assumes a direction somewhat oblique to that of the longer axis of the skull which allows the palate to broaden posteriorly.

The sectorial, or P.$\frac{4}{4}$, is exceptionally well preserved on the right side in No. 553. In form and structure it much resembles the same tooth in *Canis urostictus*, though it is proportionately a little longer antero-posteriorly than in that species and is thus a little more specialized perhaps than in that species. I think Professor Scott has somewhat exaggerated the primitive characters of this tooth, for aside from its general resemblance to that tooth in the species just cited I note that the antero-external cone as well as the posterior is quite as trenchant as in certain modern species, *Canis cancrivorus* for instance; while the antero-internal cone is proportionately no more prominent than in *Canis azaræ*, *C. lagopus*, *C. vulpes*, or certain varieties of *C. familiaris*. If we compare this tooth with that of *Prodaphænus scottii*, a supposed ancestral form known from a single series of teeth discovered by the present writer in the Uinta beds of northeastern Utah, the comparatively specialized nature of this tooth in *Daphænus* becomes even more apparent. The antero-external cone of the sectorial in *Daphænus* is highly trenchant posteriorly and pushed inward. The antero-internal cusp is small. The posterior cone is small and trenchant. The shear is oblique, a primitive character, as in *Canis cancrivorus* and most of the smaller species of modern dogs, not parallel with the longer axis of the skull as in *C. occidentalis* and the wolves generally. Surrounding the tooth there is a well-defined basal cingulum. In Fig. 4, *a*, *b*, *c* represent the superior sectorials respectively of *Prodaphænus scottii*; *Daphænus felinus* (No. 553) and *Canis lagopus*. The comparative degree of specialization of that tooth in *Daphænus* is well shown in these figures.

FIG. 4. Crown view of right superior sectorials of; *a*, *Prodaphænus scottii* W. & M. after W. & M.; *b*, *Daphænus felinus* (No 553); *c*, *Canis lagopus*. All natural size.

M.$\frac{1}{1}$ is exceptionally well preserved on both sides in skull No. 553, it is completely surrounded by a basal cingulum which is least distinct on the anterior border. The crown of this tooth is subtriangular in outline and supports three well defined cones of which two are external and one internal. The two external cones are conical in shape, subequal in size and situated well within the basal cingulum. The internal cone is crescentic in form and there is a faint indication of an anterior intermediate cone between it and the antero-external cusp. The molars of the opposite sides converge posteriorly so that the palate is widest between the posterior borders of the sectorials.

M.$\frac{2}{2}$ is much smaller than M.$\frac{1}{1}$, but has the same general pattern except that the external cones are situated nearer the outer margin of the tooth and the posterior is much smaller than the anterior.

M.$\frac{3}{3}$ is represented only by the alveolus, which indicates that this tooth was small and not functional.

MEASUREMENTS.

Length of premolar-molar series from base of canine	76 mm.
Length of molar series	38 "
Fore and aft diameter of canine at base	12 "
Transverse diameter of canine	9 "
Length of sectorial (No. 553)	16 "
Width of anterior portion of sectorial (No. 553)	10 "
Antero-posterior diameter of $M.^{1}$ (No. 553)	11 "
Greatest transverse diameter of $M.^{1}$ (No. 553)	17 "

Inferior Dentition.—With the exception of the incisors and $P._{\overline{3}}$ all the lower teeth are well preserved on one side or the other in No. 492. Neither the incisors nor their alveoli are preserved in our material, so that in giving the dental formula I have followed Leidy and Scott as to the number of lower incisors. The canines like those of the upper jaw are stout and without cutting edges. $P._{\overline{1}}$ is a very small tooth fixed in the jaw by only one root, which is directed obliquely backward. There is a rather high cusp on the anterior portion of the crown of this tooth. $P._{\overline{1}}$ is separated from the canine and the succeeding premolar by considerable diastemata. $P._{\overline{2}}$ is represented by only the fangs. $P._{\overline{3}}$ is separated from the preceding tooth by a short diastema, but is in contact with $P._{\overline{4}}$. It bears a single median cone and has the posterior portion somewhat stronger than the anterior. There is a faint indication of a basal cingulum about the posterior border. $P._{\overline{4}}$ is in contact with $P._{\overline{3}}$ and $M._{\overline{1}}$. It bears a prominent median cone and a well-defined posterior conule. There is a basal cingulum about the postero-external border of this tooth and the heel is considerably broader than the anterior portion, a character not well shown in the drawing reproduced in Pl. XVI., Fig. 4. The sectorial is well preserved in either ramus. The trigon is high and the heel low and flat. The external cusp of the trigon is much the highest and most prominent of the three, while the internal and anterior are of equal height, although the latter is much the stronger of the two. The external cusp of the talon is low and broad while the internal is faint or obsolete. There is an external basal cingulum. The crown of $M._{\overline{2}}$, as shown in Fig. 5, has the same general pattern as the sectorial except that the trigon is much lower. As in that tooth there are three anterior cones forming a low trigon and a single posterior cone on the heel. The last mentioned cone occupies a more median position than does the corresponding cone of the sectorial, while the trigon is much lower and the cusps forming it are all of equal height, though the external is much stronger than the internal and anterior. $M._{\overline{3}}$ is a convex rounded nub with a low central cone and a slightly elevated posterior cingulum.

FIG. 5. Crown view of right $M._{\overline{2}}$ of *Daphaenus felinus* (No. 492).

Measurements.

Length of premolar-molar series from alveolar border of canine	83	mm.
Length of molar series	32	"
Antero-posterior diameter of sectorial	17	"
" " " " canine	12	"
Transverse diameter of canine	8.5	"

Summary of Cranial and Dental Characters.

From the above description and the accompanying figures it will readily appear that the character of the skull, mandible and dentition of *Daphænus* is essentially canine, and although possessing a number of creodont characters, more especially in the skull, on the whole it is not very different from that which we might expect among representatives of the Oligocene canidæ. I fail to recognize those resemblances between the skull of *Daphænus* and that of the early *Machairodonts* referred to by Scott. On the other hand all the creodont characters noted by Scott are confirmed in our material, and in addition I may mention the following:

1. The unusual development of the sagittal and occipital crests, which is even more marked than in Hyænodon. Owing to the imperfect nature of the material at his command Scott erroneously described the sagittal crest in *Daphænus* as being low, it is in fact extremely high and sharp, as shown in Fig. 1.

2. The widely separated premaxillaries and frontals.

3. The incurved pterygoids, which show a tendency to arch over the posterior narial tract inferiorly as is completely done by these bones in Hyænodon.

4. The imperfect development of the auditory bulla.

5. The nearly horizontal zygomata, which are but slightly arched vertically. The orbit however is more widely open posteriorly than in most modern canidæ, and the prominently developed and deflected postorbital process of the frontals seen in *Hyænodon* are only very moderately developed in *Daphænus*.

The angular process and general conformation of the mandible as well as the limited area of the symphysial surface by which the rami are imperfectly united are essentially canine rather than feline or creodont.

While the dentition is as a whole undoubtedly more primitive than that of any single living species of dog, I do not recall any single character which could be regarded as primitive that is not paralleled or surpassed in some of the recent dogs. The character of the sectorials is very like that of those teeth in *Canis urostictus*, as has already been remarked, and is less primitive than obtains in *C. parvidens*. The dental formula, though normal for heterodont mammals, is surpassed by Otocyon,

while according to Mivart *C. cancrivorus* has been known to develop the same dental formula as *Daphænus*.

The Vertebral Column.

C. 7; D. 13?; L. 7?; S. 3; C. 23?.

Unfortunately the vertebral column was not sufficiently well preserved to permit of an accurate determination of the vertebral formula, though the principal characters of the vertebræ of the different regions, except in the sacrum and cervicals, are well shown.

The Cervicals.—Pl. XVII., Figs. 1, 2, 3. Of the cervicals only the atlas is preserved and it lacks the transverse processes and a portion of the neural arch, but is otherwise in an excellent state of preservation. It does not differ essentially from that vertebra as described by Scott in *Daphænus vetus*, except that the articular surfaces for the axis are inclined to the fore and aft axis of the vertebra at an angle of about 45°. As noted by Scott, the vertebrarterial canal perforates the base of the transverse process horizontally as in the cats, and not vertically as in the modern dogs.

The Dorsals.—Pl. XVII., Figs., 4, 5. Save the first vertebra the complete dorsal series is represented in our skeleton, though they are all somewhat injured, and in none is the neural spine complete. Compared with the skull and the lumbars the dorsals seem small and the dorsal region as a whole somewhat abbreviated. The transverse processes are robust and the neural arches and spines slope rather abruptly backward from the first to the ninth. Dorsal eleven is the transitional or anticlinal vertebra. The entire length of the dorsal series is 380 mm.

The Lumbars.—Pl. XVII., Figs. 13, 14, 15. All the lumbars are represented in our skeleton except the sixth, assuming that there were present in the skeleton seven lumbars, which is the normal number in the canidæ. The first lumbar has a well developed anapophysis which points directly backward and a little outward. The transverse processes are rather slender and are directed downward, forward and outward as in the cats, instead of being directed horizontally forward as in the dogs and bears. Compared with the dorsals the lumbars are long and heavy.

The Sacrum.—This is not represented in our skeleton, but in the Princeton material it is shown to be composed of three vertebræ.

The Caudals.—Pl. XVII., Figs. 6–12. Fifteen caudals are preserved in our skeleton. Fortunately most of these are in a good state of preservation and give a fair idea of the different regions of the tail. They indicate that this appendage was long and intermediate in character between the cats and creodonts, being somewhat

longer than is usual in the former, but absolutely and proportionately shorter than in the creodonts, Patriofelis and Hyænodon.

The most anterior vertebra of our series of caudals I regard as the first. It is short and stout, with widely expanded anterior zygapophyses bearing well developed metapophyses. The transverse processes are single, widely expanded both transversely and antero-posteriorly. They are directed outward and backward and support a considerable median prominence on the anterior edge. The top of the neural spine is wanting, but the base indicates that this process was fairly well developed. The above mentioned characters are all well shown in Plate XVII., Figs. 6 and 7. For an anterior caudal it very closely resembles that vertebra in Hoplophoneus, one of the Oligocene saber-toothed cats. But among recent carnivores it is decidedly more canine than feline in character.

I will next describe that caudal in our series which I regard as the fifth. It is shown in Plate XVII., Fig. 8. The posterior zygapophyses extend well beyond the posterior end of the centrum. The posterior transverse processes point strongly backward and outward and bear a rather prominent rugosity on the superior surface and near the external border. This vertebra is just commencing to develop an anterior transverse process and articulations for the chevrons.

The next vertebra, Plate XVII., Fig. 9, to be described from our series, appears to be the seventh caudal. In this vertebra the anterior transverse processes are well developed, being equal in expanse although more slender than the posterior. The metapophyses continue as well developed expansions of the anterior zygapophyses. There is a large foramen at the base and just in front of the posterior zygapophyses not shown in the figure.

The next vertebra to be described in our series I regard as the ninth caudal. It is shown in Pl. XVII., Fig. 10. In this vertebra the anterior of the transverse processes have become the stronger and are directed forward and outward instead of directly outward. The development of the anterior transverse process of the caudals of this region is much more marked in *Daphænus* than in most modern dogs and cats, and is quite unlike that which obtains in *Hoplophoneus*. This vertebra bears on the inferior surface at its anterior extremity very prominent rugosities for the attachment of chevrons.

Between the supposed ninth and the next vertebra represented in our series a number of caudals are missing. I have estimated the number at three. This would make the vertebra represented in Fig. 11, Pl. XVII., the thirteenth. In this vertebra the neural canal has already become obsolete, the anterior and posterior zygapophyses are reduced to mere prominences, as are also the ante-

rior and posterior transverse processes. The rugosities for the chevrons continue prominent.

Of the remaining caudals all are represented in our series but the sixteenth and one or more of the distals. The twenty-first is shown in Fig. 12, Pl. XVII. It is reduced to a slender rod of bone and is evidently from near the posterior extremity of the tail. There is only one smaller in our series.

MEASUREMENTS.

Length of centrum of first? caudal	19 mm.
Expanse of transverse process of same vertebra	61 "
Length of centrum of fifth? caudal	35 "
" " " " seventh? caudal	40 "
" " " " ninth? "	41 "
" " " " thirteenth? caudal	44 "

THE STERNUM, PL. XVIII., FIG. 1.

The sternum in our skeleton is represented by five of the mesosterni. I have interpreted these as the anterior. Assuming that there were present in the sternum of *Daphœnus* six mesosterni, the normal number alike in the canidæ and felidæ, there is wanting but one of these bones. This, together with the presternum and xiphisternum, both of which are wanting in our skeleton, would complete the sternal series. These bones are rather more slender than in recent dogs of the same size, but they are of the same general character. Their combined length is 132 mm.

THE OS PENIS, PL. XVIII., FIGS. 4, 5.

Daphœnus, as well as *Cynodictis*, was possessed of a remarkably well developed and highly specialized os penis, even surpassing that which obtains in the modern raccoons. As regards the development of this bone *Daphœnus* was preëminently canine rather than feline in character.

The os penis, throughout the proximal two thirds of its length, is elliptical in cross-section with the greater diameter directed vertically. Proximally, it is much compressed into a flattened, wedge-shaped, very rugose extremity, for muscular attachment to the pubes. Distally, this bone becomes more cylindrical in cross-section, and at about the middle of its length a shallow groove appears on its inferior surface. This gradually becomes more pronounced, giving rise anteriorly to a deep channel, and at a distance of 10 mm. from the extremity the bone is entirely bisected, and sends forward the two peculiar spout-like processes shown in Fig. 5, Pl. XVIII., each with a shallow groove on its internal surface.

In *Cynodictis* this bone is grooved throughout nearly its entire length. The distal extremity is not bifurcated as in *Daphœnus*, but is solid, abruptly curved, and terminates in much the same manner as in *Procyon lotor*. The dimensions of these bones in *Daphœnus* and *Cynodictis* are as follows:

Length of os penis in Daphœnus	166 mm.
" " " " Cynodictis	120 "
Depth of os penis in Daphœnus at proximal end	16 "
" " " " Cynodictis " "	9 "

The Ribs.

Most of the ribs are represented and several are quite complete. The anterior are short but proportionately very stout. Throughout the series they are shorter than in most modern dogs, with limbs of equal length, thus indicating a body cavity of relatively small capacity. The greatest length of the best preserved ribs measured along the cords of the arcs formed by the bones is as follows:

First	45 mm.
Second	58 "
Third	83 "
Fourth	98 "
Sixth	105 "
Seventh	119 "
Ninth	123 "
Tenth	120 "

The Fore Limbs and Feet.

Unfortunately the scapulæ are wanting in our skeleton and I am unable to give the characters of this important bone.

The Humerus.—Pl. XIX., Figs. 7, 7ª and 8. Both humeri are preserved in our skeleton and are nearly complete, though much crushed. They are decidedly more cat-like than canine. In fact almost every character by which one could with reasonable certainty distinguish a modern feline humerus from that bone in the canidæ is present, and were the humerus of *Daphœnus* found isolated one would unhesitatingly refer it to some member of the felidæ, thus showing how unreliable a guide the comparative osteology of recent vertebrates may be to the student of vertebrate paleontology. There is a large *supra-condyloid foramen* bounded internally by a strong supra-condylar ridge, a character always found in the modern felidæ and which would alone distinguish the humerus of a cat from a dog. There is no *supra-trochlear foramen*, but the anconeal fossa is deep. The external *supinator ridge* is developed into a broad and sharp ridge of bone ex-

tending throughout about one third the total length of the shaft. Superiorly this ridge shows a much greater development than in either the modern felidæ or canidæ. The articular surface of the radial condyle is more distinctly keeled than in the felidæ and in this respect is more canine in character. A very sharp ridge continues upward from this keel along the posterior side of the bone and along the external margin of the anconeal fossa. The ulnar condyle is somewhat intermediate between that which obtains in the modern canidæ and felidæ. Proximally the deltoid ridge is only moderately developed. The bicipital groove is deep as in the dogs, the head is subelliptical in outline with the greater tuberosity much exceeding the lesser in size.

The Radius and Ulna.— Pl. XIX., Figs. 9–12. Both radii are present and in good condition. The most remarkable feature of the bones of the forearm is their diminutive length as compared not only with the humerus, but with the same bones in modern canidæ and felidæ, more especially the former. While the lengths of the humerus and radius in the present skeleton are respectively 185 mm. and 135 mm., the latter being therefore a little more than one fourth shorter than the former I note that the relative lengths of these bones in *Felis tigris* and the retriever dog are respectively 270 mm. and 240 mm. and 183 mm. and 205 mm. Thus we see that in the tiger the radius is only one ninth shorter than the humerus, while in the dog it is nearly one eighth longer than the humerus. In *Canis latrans* the lengths of these bones are 157 mm. for the humerus and 163 mm. for the radius, the radius being still somewhat longer than the humerus. These bones are not only proportionately shorter than in the canidæ, but they are stouter and more completely crossed than in the dogs. In both these characters they resemble more closely those conditions as found in the cats than in the dogs. The articular surface of the head of the radius for the humerus is regularly concave and rather deeper than in the dogs and suboval in outline. The inner margin of the head is much expanded and overhangs the shaft of the bone as in the cats. Anteriorly there is a small median prominence. The surface for articulation with the lesser sigmoid cavity of the ulna is carried far around on the internal side of the head of the radius by reason of the enlarged coronoid process of the ulna which is feline rather than canine in character. The tubercle of the radius is rather prominent and there is a noticeable constriction between it and the head. On the postero-external side, and in about the middle of the shaft of the radius there is an elongated rugosity which opposes a similar one on the antero-external surface of the ulna. These rugosities served for the muscular attachment of these bones. The distal end of the radius is considerably expanded both antero-posteriorly and transversely and supports a triangular,

shallow, cup-like articular surface for contact with the scapho-lunar. This articular surface is continued far down on the styloid process. There is a rather deep groove for the extensor tendon of the pollex and just above this and on the internal side of each radius is a remarkable exostosis. On the anterior and external surface of the distal end of the radius are to be seen the usual grooves for the extensor tendons of the manus. The articular surface for the distal end of the ulna is nearly circular in outline and occupies the same position as in the cats, being decidedly more inferior than that which obtains in the dogs. The shaft of the radius throughout its entire length is subelliptical in cross-section. The shaft of the ulna is much compressed proximally as in the cats, not trihedral as in the dogs. The olecranon process is broad and higher than in the modern dogs, though perhaps not quite so prominent as in the cats. It may therefore be considered as somewhat intermediate in character between the dogs and cats though decidedly more like the latter. The superior and posterior margins of the olecranon are very rugose and much expanded, indicating the presence of a powerful triceps muscle. The greater sigmoid cavity does not differ much from that which obtains in modern dogs. What little variation there is however is seen in the more extended inferior and internal articular surface, due to the greater development of the coronoid process and is in the direction of the cats. Indeed the entire construction of the elbow and limb is remarkably feline as is seen in the abbreviated forearm, the well-developed coronoid and olecranon processes of the ulna and the presence of a supracondylar foramen in the humerus. Distally the ulna is trihedral in cross-section and there is a moderately developed and flattened styloid process for articulation with the pyramidal and pisiform. On the inner side at the distal end of either radius there is a considerable growth of diseased bone, or exostosis mentioned above. These are remarkably similar on either side as is shown in Pl. XIX.

The Carpus.—Pl. XVIII., Fig. 10. The carpals of the right manus are all present in our skeleton with the exception of the pyramidal. While that bone is wanting in the right manus it is present in the left, so that it is possible to determine with accuracy the structure of the carpus. The proximal series of carpals consists of the coössified scapho-lunar, the pyramidal and pisiform. In the distal row there are the usual elements, the trapezium, trapezoid, magnum, and uneiform.

The scapho-lunar is much the largest bone in the carpus. The two elements of which it is made up are so completely united as to leave no trace of a suture. The radial side is a little more depressed than in canis, while the posteriorly-projecting *radiopalmar process* is reduced as in the cats instead of expanded vertically as in the dogs. Superiorly there is a regularly convex articular surface for articulation with

the radius, while distally there are four well-defined articular surfaces for contact with the trapezium, trapezoid, magnum, and unciform. The scapho-lunar did not articulate laterally with the pyramidal as in the canidæ, but those bones were well separated by the superior, keeled, articular surface of the unciform. The middle, inferior, and anterior surface of the scapho-lunar is produced into a rather extended keel, which is interposed between the trapezoid and external portion of the magnum in such manner as to reduce the antero-internal portion of the latter to a flattened disk, more pronounced even than in the modern felidæ and quite different from that which obtains in the dogs.

The pyramidal is very much flattened, much more so than in either the recent canidæ or felidæ. Inferiorly and posteriorly it is continued into a considerable process which overlaps and gives lateral support to the proximal end of metacarpal V. Inferiorly there is a rather extensive and concave surface for articulation with the unciform. The superior, or external surface, shows two subequal articular surfaces, separated by a low keel for contact with the pisiform and ulna.

The pyramidal and ulnar articular surfaces of the pisiform are subequal and the tuberosity is more expanded than in either the modern canidæ or felidæ.

The trapezium is decidedly heavier than the trapezoid in marked contrast to the relative proportions of those bones in the modern dogs. It presents a broad, flat articular surface for contact with M. I., but scarcely articulated with M. II. thus approximating the dogs rather than the cats.

The trapezoid is a small triangular bone with the apex directed backward. Superiorly it presents to the scapho-lunar an articular surface which is convex anteriorly and concave posteriorly. On the internal side it articulates with the trapezium, while inferiorly and externally it articulates with M. II. and the magnum, which it slightly overlaps as in the cats, though its contact with the latter bone is quite limited. The general shape of the bone is cat-like rather than canine.

The magnum is very much depressed antero-internally, but externally it sends upward a sharp ridge of bone between the unciform and scapho-lunar which posteriorly almost entirely separates those bones. Both these characters are feline rather than canine, but both are more emphasized in *Daphœnus* than in the recent cats, while in the dog the magnum is high in front throughout its entire width and the superior keel or ridge on the supero-external border is less pronounced than in the cats. Distally the magnum presents an articular surface for contact with M. III.

Next to the scapho-lunar the unciform is the largest bone in the carpus. It is wedge-shaped, with the apex directed upward. It articulates internally with the magnum and scapho-lunar, externally with the pyramidal and distally with M. IV.

and V. It is proportionately broader and lower than in the cats. In this respect it approximates more nearly those conditions which obtain in the dogs, but it is much more compressed superiorly than in the dogs, thus resembling the cats. It is, in fact, intermediate in form between that which obtains in the dogs and cats, though approaching somewhat more nearly the latter.

Considered as a whole, the carpus of *Daphœnus* seems remarkably cat-like, but proportionately a little low and broad, the trapezoid and magnum being especially reduced in height. It is, therefore, of quite primitive structure and indicates that *Daphœnus* had not yet acquired cursorial habits.

The Metacarpus.—Pl. XVIII., Fig. 10. In *Daphœnus* the metacarpus is short and broad as compared with that of either the dogs or cats. Metacarpal I. is longer when compared with the other metacarpals than in the recent dogs or cats. Its articulation with the carpus is decidedly feline. It articulates with the trapezium only, the lower portion of that bone being interposed between the proximal ends of Metacarpals I. and II. in such manner as to exclude the former from contact with the latter precisely as in the cats. Metacarpals II., III., IV. and V. are of about equal strength. III. and IV. are the longer and are subequal in length while II. and V. are of about equal length but noticeably shorter than III. and IV. Metacarpals II., III., IV. and V. are closely applied proximally, but somewhat separated distally. The proximal inter-articulation of these bones is much less complicated than in the cats or dogs and they do not so perfectly interlock with one another as in either of the latter, showing that the manus of *Daphœnus* was less perfectly digitigrade than that of recent dogs, though by no means plantigrade. The proximal articulation of these bones with one another is decidedly more canine than feline.

The Phalanges.—Pl. XVIII., Fig. 10. The phalanges are intermediate in character between those of the dogs and cats. Those of the proximal row are somewhat arched as in the cats. The second series are nearly symmetrical as in the dogs, but the distal articular surfaces are less expanded laterally than in the dogs and are continued further back, upon the superior surface, as in the cats, indicating that the terminals were to a certain extent at least retractile. The terminal phalanges are high and very much compressed claws with rudimentary hoods. They are distinctly cat-like rather than canine in character.

Taken as a whole, the forelimb and foot of *Daphœnus* was comparatively short, the forearm and foot especially so. In general, its structure is decidedly feline rather than canine, and this applies alike to the bones of the brachium, the antebrachium and the manus, though there are a few canine characters, more especially

in the structure of the manus and the character of the proximal and second series of phalanges.

PRINCIPAL MEASUREMENTS OF FORE LIMB AND MANUS.

Greatest length of humerus	185 mm.
" transverse diameter of distal end of humerus	41 "
" length of radius	135 "
" " ulna	171 "
" " ulna below coronoid process	137 "
Height of olecranon above anconeal process	27 "
Antero-posterior diameter of olecranon at summit	22 "
" " ulna just below sigmoid cavity	20 "
Greatest breadth of carpus	34 "
Greatest height of carpus, anterior	12 "
" breadth of scapho-lunar	24 "
" depth of scapho-lunar	10 "
" length of metacarpal I.	25 "
" " " II.	37 "
" " " III.	47 "
" " " IV.	45 "
" " " V.	35 "
Combined length of phalanges of digit I., when in position	29 "
" " " " II., " " "	46 "
" " " " III., " " "	54 "
" " " " IV., " " "	52 "
" " " " V., " " "	45 "

THE HIND LEG AND FOOT.

Unfortunately the pelvis is not preserved in our skeleton. All the bones of either hind leg and foot however are present and in a good state of preservation, with the exception of some three or four phalanges.

The Femur.—Pl. XIX., Figs. 1 and 2. When compared with the humerus, the femur of *Daphaenus* is proportionately a little shorter than in either the dogs or cats. The head is directed more vertical than in either of the latter animals. The depression for the *ligamentum teres* is situated well down toward the lower margin of the articular surface of the head. The neck is constricted and extends inward and upward at an angle of about thirty degrees to the vertical axis of the bone, so that the position of the head is much less horizontal than in recent dogs or cats. The greater trochanter is a little lower than the superior surface of the head. Posteriorly and superiorly it is produced into a sharp ridge which partially encloses the deep digital fossa. Externally it is expanded into a broad, rugose area for muscular attachment. Vertically this rugosity is much more extensive than in modern forms and inferiorly it is continued as a sharp ridge of bone extending along the

posterior external border throughout one half the length of the bone. On the postero-internal margin, just at the base of the neck, there is a conspicuous *lesser trochanter*. There is no third trochanter. Distally the internal and external condyles are subequal and separated by a deep but narrow intercondylar notch. There were present on the external condyles rather prominent fabellæ. The external and internal tuberosities are not prominent and in the middle of the latter there is a deep ligamentary depression, equaling that for the *ligamentum teres*. The trochlea for the patella is broad and shallow as in the cats.

The Patella.—Pl. XIX., Fig. 13. This bone is decidedly feline in character. Its general form is that of an almond, thickened above and wedge-shaped inferiorly. The articular surface is broadly convex transversely and very gently concave vertically.

The Crus.—The crus is in almost every respect more feline than canine in character. This is shown in the length of the bones composing it, which are not only absolutely longer than those of the fore arm, but are proportionately longer when the length of these bones is compared with that of the humerus and femur. But it is in the shape of the fibula and in its relation to the tibia that the most characteristic feline characters are to be found, as will readily appear when we come to describe that bone in detail.

The Tibia.—Pl. XIX., Figs. 3 and 4. The tibia is a little more than one fourth longer than the radius. Proximally it is much expanded both laterally and anteroposteriorly. The surfaces for articulation with the external and internal condyles of the femur are subequal and separated from one another by a rather high median crest. The cnemial ridge is high and long, extending far down on the anterior border, as in the cats, instead of being short as in the dogs. There is a broad articular area on the inferior and outer surface of the external tuberosity for articulation with the fibula. The external and internal tuberosities are much projected posteriorly in such manner as to overhang the shaft of the bone to a much greater degree than that which obtains in the dogs and more nearly resembling those conditions as displayed in the cats. Throughout the proximal two thirds of its length the shaft of the tibia is trihedral in cross-section, distally, however, it is irregularly quadrangular. Throughout one half of its length at the distal extremity the external surface of the tibia is produced into a low sharp ridge, as in the cats, instead of being flattened for contact with the fibula, as in the dogs. In harmony with the above mentioned characters the shafts of the tibia and fibula are widely separated in *Daphænus* throughout their entire length as in the cats, instead of being closely applied throughout the lower one half of their length as in the dogs. The distal

articulation for the fibula is small. Internally the distal end of the tibia is produced into a broad internal malleolus. The grooves for the flexor tendons are fairly well defined. The ridge separating the external and internal articular surfaces for the astragalus is low as in the cats and the external surface is transversely broader than the internal, though the latter is more extended antero-posteriorly.

The Fibula.—Pl. XIX., Figs. 5 and 6. This bone is cat-like in almost all its characters. The shaft is very slender and much flattened transversely. The proximal end is much expanded, with a deep external concavity embraced between prominent anterior and posterior rugose tuberosities, while on the internal side there is a sharp median ridge extending for an inch below the ovate articular surface for the tibia. For a short distance below the termination of this ridge the shaft becomes a slender, cylindrical rod of bone, circular in cross-section, a little below this its antero-posterior diameter increases and it becomes a flattened bar with the external surface gently convex. Distally the fibula is expanded in both directions. On the postero-inferior angle there is an external malleolus, while just below and a little anterior to this is a prominent tuberosity, as seen in some of the cats, though absent in others and in the dogs generally. A deep groove for the *peroneus longus* is thus formed between this tuberosity and the external malleolus. The articular surface for the tibia is small, that for the astragalus is much larger. On comparing this bone with the fibula of *Hoplophoneus*, a contemporaneous sabre-toothed cat, I note that it resembles more closely that of the modern felines. While the fibula of Hoplophoneus is distinctly feline, yet it bears a certain resemblance to that bone in the creodonts not shown by the fibula in Daphœnus. These resemblances are to be seen in the shorter and more cylindrical shaft and in the rather less expanded extremities.

The Tarsus.—Pl. XVIII., Fig. 9. The tarsus of Daphœnus and indeed the entire pes is decidedly feline rather than canine in structure, and moreover it more closely resembles the pes in modern cats than does the pes of *Hoplophoneus*. All the elements usually found in the tarsus of the carnivora are present.

The calcaneum is comparatively rather short and stout. The tuberosity is more expanded antero-posteriorly than in the modern cats or *Hoplophoneus*. On its anterior surface midway between the summit and the articular surface for the astragalus there is a prominent rugosity. At the apex the internal tuberosity is more elevated than the external and they are separated by a shallow median groove for the *tendon of Achilles*. Compared with modern dogs or cats the inferior portion of the calcaneum is remarkably short and broad. The external articular surface for the astragalus is flat transversely, but very convex supero-inferiorly. It is continued

well up on the antero-internal surface of the tuberosity, as in recent dogs and cats. The *lesser process* or *sustentaculum* is much more expanded than in either the dogs or cats. It bears the internal articular surface for the astragalus. This surface is elliptical in outline. Superiorly it is separated from the external articular surface by a shallow groove for the interosseous ligament, and inferiorly by a rather wide rugose area. The *greater process* is much broader and shorter than in recent dogs and cats and shows no articular surfaces for the neck and head of the astragalus. The *peroneal tubercle* is more prominent than in recent cats and the groove for the *peroneus longus tendon* is deeper. The articular surface for the cuboid is subcircular, regularly concave and looks almost directly downward as in the dogs instead of downward and inward as in the cats. There is a large, rugose tuberosity on the posterior side of the distal end. Owing to the abbreviated nature of the distal portion the calcaneum does not come in contact with the navicular.

The astragalus is feline throughout. The head is much expanded transversely and the neck is even more constricted than in most modern cats. The neck and head are inclined sharply inward from the axis of the trochlea and the head presents an elongated, elliptical articular surface for the navicular, which is convex in all directions. The trochlea is not so convex supero-inferiorly as in the recent canidæ or felidæ, but in other respects it does not differ materially from that surface in the cats. The tibial side is low and narrow, the fibular high and wide, and they are separated by a wide ginglymoid groove which may be a little shallower than in the modern cats, but is decidedly deeper than in *Hoplophoneus*. On the plantar side the external and internal articular surfaces for the calcaneum are separated by a deep, narrow groove for the *interosseous ligament*. These articular surfaces do not differ from the corresponding ones in the astragalus of the cat.

Owing to the abbreviated *greater process* of the calcaneum and the unreduced neck and head of the astragalus the inferior surface of the latter falls below the inferior portion of the calcaneum and comes in contact laterally with the cuboid, a condition which, in so far as I know, does not obtain in either the dogs or cats of the present day, but is to be observed, though to a less extent, in *Hoplophoneus*. By reason of the abbreviated nature of the inferior portion of the calcaneum, which thus allows the cuboid to articulate laterally with the ectocuneiform, the navicular and the head of the astragalus, the cuboid is proportionately elongated in *Daphœnus*. Its superior surface for articulation with the calcaneum is regularly but gently convex. Inferiorly it articulates with metacarpals IV. and V. by a single, slightly concave articular surface. On the internal side there are two articular surfaces for contact with the ectocuneiform, separated by a broad, shallow groove. One of these

is very small and is situated on the lower antero-internal angle, the second and larger is triangular in outline and occupies the antero-median portion of the internal border. On the supero-posterior angle there is a small surface for contact with the navicular, while extending all along the supero-internal border is a surface for the head of the astragalus. On the tibial side there is a well-developed tuberosity running obliquely across the surface of the bone. This is separated from the inferior and dorsal surfaces by a deep groove for the *peroneus longus*. These conditions are just such as obtain in the cat, but quite different from those found in the dog.

The ectocuneiform is in general cat-like, but with a number of distinctive characters. The distal surface is more distinctly concave antero-posteriorly and transversely, and the posterior projection is not so much constricted. On its external side it articulates with the cuboid and metatarsal IV. Internally, besides articulating with the mesocuneiform, it has an extended contact with metatarsal II. Superiorly it articulates with the external one half of the inferior surface of the navicular. The process of the posterior surface is less hooked than in the cats and decidedly more like that of the dogs.

The mesocuneiform is much the smallest bone of the tarsus. It is wedge-shaped with the apex directed posteriorly. Both the superior and inferior surfaces are concave, the former articulates with the navicular, the latter with metatarsal II. Externally it articulates with the superior one half of the internal side of the ectocuneiform, internally with the superior portion of the external surface of the entocuneiform.

The entocuneiform does not differ materially from that bone in recent carnivores. It is elongated vertically and wedge-shaped antero-posteriorly. Externally it articulates with metatarsal II. and the mesocuneiform, proximally with the navicular, and distally it gives support to metatarsal I., which is much less reduced than in the recent dogs and cats.

The navicular in *Daphœnus* is low as in the cats. The superior surface is deeply concave for the reception of the convex head of the astragalus. Inferiorly it articulates with all three of the cuneiforms, but the articular surfaces for each are only indistinctly differentiated. There is a pronounced posterior tuberosity.

The Metatarsus. — Pl. XVIII., Fig. 9. The bones of the metatarsus interlock much more perfectly than do those of the metacarpus. While differing in some of its details from that of the cats, the metatarsus is decidedly feline rather than canine. This is seen in the greater development of the tuberosity of metatarsal V.; in the more produced proximal portion of metatarsal II., so as to articulate or cover throughout one half its length the inner surface of the ectocuneiform, and in the

arched palmar surface of all the metatarsals. In *Daphœnus* metatarsal I. is present and bears two well developed and functional phalanges, thus differing materially from both the recent cats and dogs. The articulation between the proximal ends of the metatarsals and the distal row of tarsals is more complicated than in either the cats or dogs. This is due to a system of "breaking joints" as it were, well shown in the figure. The entocuneiform, besides articulating externally with the mesocuneiform, has a quite extended contact with the internal surface of the proximal end of metatarsal II., while the latter, as already remarked, externally overlaps the lower one half of the internal side of the ectocuneiform. The proximal end of metatarsal IV. rises above metatarsal III. and articulates with the extreme distal, external lateral surface of the ectocuneiform. The distal extremities of the metatarsals are expanded dorsally just above the articular surfaces into prominent rugose tuberosities as in the cats.

The Phalanges.—Pl. XVIII., Fig. 9. The proximal phalanges are arched as in the cats, save that of digit I. which is comparatively straight. The second series of phalanges are less symmetrical than the same series in the manus, and approach more nearly the form assumed by that series in the modern cats. As in the cats the outer border is the thicker, and the distal articular surfaces are directed somewhat externally. The unguals are developed into sharp-pointed, high, compressed, hooded claws, as in the cats, instead of curved cylindrical cones as in the dogs. As in the fore foot the structure of the unguals and second series of phalanges indicates that *Daphœnus* was provided with retractile claws much as the modern cats. There were but two phalanges in the first digit. Taken as a whole the pes of *Daphœnus* was a little shorter and broader than that of the modern cats, and decidedly more so than that of the recent dogs. It was much longer however than in the machairodonts. There were the usual sesamoids, both in the fore and hind feet, but they present no peculiarities and hence need no further description.

Principal Measurements of Hind Leg and Foot.

Greatest length of femur	201	mm.
Expanse of condyles	32	"
Greatest length of patella	21	"
" breadth of patella	16	"
" thickness of patella	8	"
" length of tibia	179	"
Distance from posterior border of external trochlea to summit of cnemial crest	41	"
Transverse diameter of proximal end of tibia	36	"
" " distal end of tibia	28	"
Depth of internal malleolus below internal groove for astragalus	13	"
Length of fibula	168	"

Breadth of fibula at proximal end	22 mm.
" " distal end	16 "
Length of calcaneum	50 "
Height of tuberosity of calcaneum above groove for interosseous ligament	34 "
Depth of greater process below groove for interosseous ligament	16 "
Distance from internal border of lesser process to external border of peroneal tubercle	28 "
Antero-posterior diameter at base of tuberosity	20 "
Greatest length of astragalus	30 "
" breadth of astragalus	21 "
Transverse diameter of head of astragalus	17 "
Distance of head below inferior margin of ginglimoid groove	15 "
Height of cuboid	16 "
" ectocuneiform	11 "
" mesocuneiform	6 "
" entocuneiform	14 "
Depth of navicular	8 "
Transverse diameter of navicular	21 "
Length of metatarsal I	35 "
" " II	49 "
" " III	58 "
" " IV	61 "
" " V	50 "
" phalanges of digit I. in position	33 "
" " " II. "	47 "
" " " III. "	56 "
" " " IV. "	55 "
" " " V. "	47 "

After the above description of the skeleton of *Daphœnus felinus* was written, it was carefully compared with the osteological characters as described by Professor Scott and a number of inharmonious statements were detected relating to those parts of the skeleton preserved in the collections of both museums. A careful reëxamination of our material was then undertaken with the idea of eliminating if possible such inconsistencies. This attempt, however, was only partially successful, for while a number of inaccuracies were found in my first description they were for the most part unimportant and there still remain a number of differences between the description given above and that of Scott. Many of them are doubtless due to the imperfect, fragmentary and scattered condition of the material upon which Professor Scott's description was based, which frequently did not permit of an accurate determination of certain characters.

The Mounted Skeleton. Plate XX.

The skeleton (No. 492) was freed from the matrix with great skill and care by Mr. O. A. Peterson and has been mounted with commendable ingenuity by Mr. A.

S. Goggeshall in such manner that all the different bones may be readily detached for examination and study. The pelvis, sacrum, missing lumbar and cervicals were modeled from material very kindly loaned by Dr. M. S. Farr, Curator of Vertebrate Paleontology at Princeton University. The scapulæ have been modeled in plaster and are purely conjectural, that element in Daphœnus remaining as yet unknown. In modelling the scapula that of the cat has been followed rather than the dog. Since in most skeletal features, aside from the dentition and skull, Daphœnus, as has been shown, is decidedly more cat-like than dog-like.

The general aspect of the articulated skeleton is that of a long, slender-bodied, long-tailed and proportionately short-limbed carnivore. In form and general proportions the appearance of the skeleton is that of a cat with a skull elongated as in the dogs. The limbs are short in proportion to the length of the skull and vertebral column. The lumbar region is especially long and the lumbars exceptionally heavy. The proportion of the axial to the appendicular skeleton is somewhat intermediate between that which obtains in the cats and creodonts.

DAPHŒNUS DODGEI Scott.

In our collections there is a left mandibular ramus (No. 573), which from its massive nature, the character of the dentition and the horizon, Titanotherium beds, in which it was found, I do not hesitate to refer to the above species. The ventral border is hardly so sinuous as that described or figured by Scott, but in almost every other respect it agrees accurately with Scott's description of the type. The teeth are placed more closely than in any of the other species, the premolars being separated from each other and the canine by very short diastemata. The premolars and molars are short but broad and $P.\frac{3}{3}$ and $\frac{4}{4}$ have well developed posterior tubercles and basal cingula. $M.\frac{3}{3}$ is implanted in the ascending ramus as indicated by the alveolus, the tooth being wanting in the present specimen.

PROAMPHICYON NEBRASCENSIS gen. et sp. nov.

Among the material collected by Mr. Peterson is an imperfectly preserved skull without lower jaw, a side view of which is shown in Fig. 6, which I have reluctantly made the type of a new genus and species. Not only does it differ materially in several important dental characters from any of the White River canidæ yet described, but moreover it presents characters quite distinct from those of *Daphœnus* and somewhat intermediate between those of that genus and of *Amphicyon*, as will be shown later.

Proamphicyon nebrascensis. — *Char. gen.* I.$\frac{3}{3}$, C.$\frac{1}{1}$, P.$\frac{4}{4}$, M.$\frac{3}{3}$. Sagittal and occipital crests very high and sharp. Premolars much reduced in size. Canines long, compressed, elliptical in cross-section and with posterior cutting edge.

Char. sp. Temporal constriction very marked and situated posterior to the anterior extremity of the sagittal crest. Capacity of brain-case much reduced. M.^{3} supported by two roots, its position more external than in *Daphaenus*. Shear of superior sectorial a little less oblique than in most other Oligocene canidæ. Internal cone of sectorial reduced. P.$\frac{1}{1}$, $\frac{2}{2}$, $\frac{3}{3}$ much compressed and without even rudimentary posterior tubercles. Incisors very small.

Detailed Description of Type (No. 491).

The type of the present genus and species consists of a skull without lower jaw or other parts of the skeleton. It is complete save for the zygomata, the posterior portion of the sagittal crest, and the basicranial region between the pterygoids and the paroccipital processes. All the teeth are represented and in an excellent state of preservation save M.^{3} and I.^{3} and the extreme point of the canine. The specimen was found by Mr. O. A. Peterson, in the Oreodon beds, on Bad Land Creek, in Sioux Co., Nebraska.

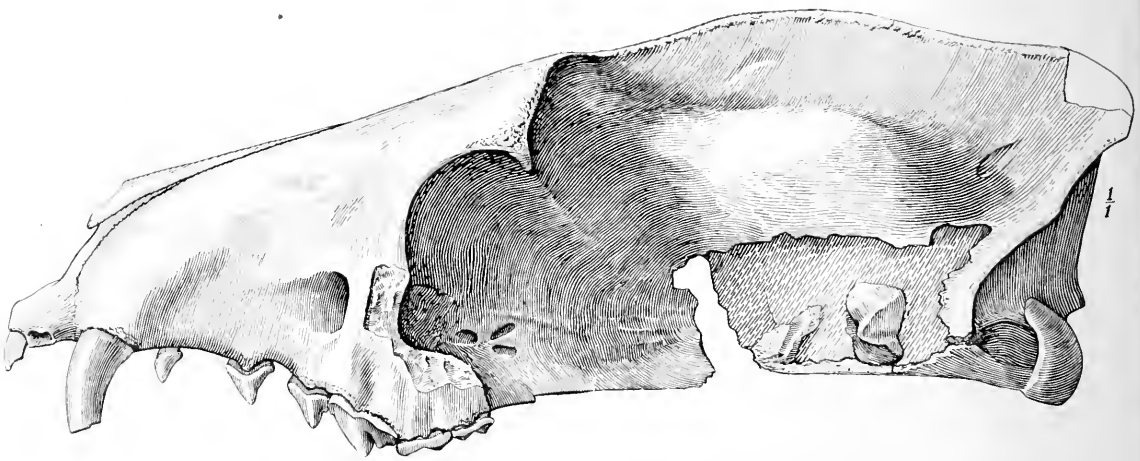


Fig. 6. Side view of type of *Proamphicyon nebrascensis* Hatcher (No. 491). Natural size.

The skull is long and compressed with the facial region somewhat less abbreviated than in *Daphaenus*. The capacity of the brain-case is rather less than in *Da-*

phœnus, while the sagittal and occipital crests are high and sharp. The sagittal crest extends a little farther forward than in that genus, while the frontals are not so broad, but somewhat longer. The occipital condyles are set obliquely, they are not much expanded and are overhung by the occipital crest. The foramen magnum is higher than wide, though this may have resulted from crushing. The basicranial region is so injured that it is impossible to determine any of its characters. The anterior palatine foramen is rather small. The anterior border of the posterior nares is on a line with the posterior border of M.$\frac{3}{}$.

The Dentition.—I.$\frac{1\&2}{}$ are small and very much compressed. I.$\frac{3}{}$ is wanting in our specimen on both sides, the alveoles show it to have been decidedly larger than I.$\frac{1\&2}{}$, but proportionately much smaller than in most recent dogs. The canine is large and elliptical in cross-section with a cutting posterior edge. It is longer and more slender than in *Daphœnus* and more nearly resembles the same tooth in *Amphicyon americanus* as described and figured by Wortman.[8] The character of this tooth is intermediate between that which obtains in *Daphœnus* and *Amphicyon*, although decidedly more like *Amphicyon*, as shown by the presence of a posterior cutting edge and its elliptical cross-section.

The three superior anterior premolars are all greatly reduced in size as shown in Fig. 7, a character also shown by *Amphicyon americanus*, according to Wortman's description, though not so apparent in his figures. The reduced size of these premolars is proportionately more pronounced than in any fossil dog I have yet seen, it even equals that which obtains in *Canis parvidens* among recent dogs. Premolars $\frac{1\&2}{}$ are separated from one another by a long diastema, and a somewhat shorter diastema intervenes between the canine and P.$\frac{1}{}$, while the space between P.$\frac{2\&3}{}$ is still less. Posteriorly P.$\frac{3}{}$ is in contact with the sectorial. The crowns of all three of these teeth consist of a single simple median cone without anterior or posterior tubercles. Premolar $\frac{1}{}$ is fixed by one root only, $\frac{2\&3}{}$ by two roots. Premolar $\frac{3}{}$ is set obliquely in the jaw. In all three of these teeth the anterior and posterior transverse diameters of each tooth are equal.

The sectorial or P.$\frac{4}{}$ is proportionately long and narrow. The anterior portion is not so broad as in *Daphœnus* and the internal cusp is low, a little more reduced than in *Daphœnus*, but not so much as in *Canis occidentalis* and the wolves generally. The proportions of this element are about the same as those which obtain in *C. lagopus* and certain others of the smaller recent dogs and foxes, as will be seen by a comparison of Fig. 4^c with Fig. 7. The antero-external or principal cone is high and directed slightly backward. It is separated from the posterior cutting

[8] See Am. Jour. Sci., Vol. II, 1901, pp. 200–204.

blade by a rather deep groove. The latter element is low, sharp and oblique in position.

Molars $\frac{1\&2}{}$ are proportionately broad transversely and short antero-posteriorly. Each of these teeth supports two subequal external cones separated by a rather deep depression from a single crescentic internal cusp at the base of which is a broadly expanded basal cingulum. Strong basal cingula are also developed on the external sides of $M.^{\frac{1\&2}{}}$, more especially $M.^{\frac{1}{}}$, and on the antero-external angle this is developed into a considerable prominence. $M.^{\frac{3}{}}$ is wanting on both sides of our specimen, but on the left it is represented by two alveoli, as shown in Fig. 7. These show it to have been rather large for a third molar and to have been aligned with the external margins of molars $^{1\&2}$.

FIG. 7. Crown view of superior dentition of type of *Proamphicyon nebrascensis* Hatcher (No. 491). Natural size.

MEASUREMENTS OF TYPE (No. 491).

Length along palate and base of cranium from incisive alveolar border to opening of foramen magnum	175	mm.
Greatest height of sagittal crest	25	"
Length of sagittal crest, estimated	92	"
Distance along median line from union of superciliary ridges to anterior extremity of nasals	86	"
Distance from posterior border of $M.^3$ to anterior border of $I.^1$	85	"
Antero-posterior diameter of canine at base	9.5	"
Transverse " " " "	6.5	"
Length of premolar series	37	"
" sectoral	12.5	"
" molar series	26	"
Antero-posterior diameter of $M.^1$	11	"
Transverse diameter of $M.^1$	16	"

RELATIONS OF PROAMPHICYON NEBRASCENSIS.

After a careful comparison of the type of the present genus and species with Wortman's description and figures of *Amphicyon americanus* already referred to, the writer believes that the skull which forms the type of the present genus and species pertained to an animal intermediate in character between Daphœnus and Amphicyon and which stood in the line directly ancestral to the latter genus. The

most important resemblances between the present genus and Amphicyon are to be found in the dentition and have already been noticed. These may be recapitulated as follows:

First: Canine elliptical in cross-section or flattened transversely and with posterior cutting edge.

Second: Premolars $\frac{1}{1}, \frac{2}{2}, \frac{3}{3}$ much reduced in size.

Third: Superior sectorial long and narrow.

Fourth: Molars $\frac{1 \& 2}{1 \& 2}$ much expanded transversely.

Fifth: Molar $\frac{3}{3}$ large, as indicated by presence of two alveoli, and aligned with external border of M. $\frac{1 \& 2}{1 \& 2}$.

The cranial characters of the American species of Amphicyon are not sufficiently well known to permit of a comparsion of these characters in the two forms. Judging from the dental characters alone however the present genus would appear to fulfill all the requirements that we might reasonably except to find in a White River ancestor of the Miocene form, except that P.$\frac{1}{1}, \frac{2}{2}, \frac{3}{3}$ are perhaps a trifle too much reduced in size. I therefore for the present regard *Proamphicyon nebrascensis* as ancestral to *Amphicyon americanus*.

PROTEMNOCYON INFLATUS, gen. et sp. nov., Plate XV.

Among the material collected by Mr. Peterson is a beautifully preserved skull (No. 552) with lower jaw, for which, from its evident relation to *Temnocyon*, I propose the genus *Protemnocyon*. In reference to the capacious nature of the brain cavity it is proposed to designate the species as *P. inflatus*.

Char. Gen. — Sagittal crest very low throughout the anterior two thirds of its length. Brain-cavity much inflated, indicating a brain one half larger in proportion to the size of the skull than that of Daphœnus or Proamphicyon. Dental formula, I.$\frac{3}{3}$, C.$\frac{1}{1}$, P.$\frac{4}{4}$, M. $\frac{3}{3}$ or $\frac{2}{2}$. Heel of inferior sectorial and M.$\frac{3}{3}$ imperfectly keeled.

Char. sp. — Temporal constriction anterior to union of superciliary ridges. Frontals broad, gently concave medially, but convex laterally, indicating the presence of well-developed frontal sinuses. Inferior margin of mandible nearly straight. M.$\frac{3}{3}$ much reduced in size or absent. P.$\frac{1}{1}$, $\frac{2}{2}$, $\frac{3}{3}$, $\frac{4}{4}$ large and with broad heels.

Detailed Description of Type (No. 552).

The type of *Protemnocyon inflatus* consists of a skull with lower jaw, atlas, axis, and third cervical found in position in the Oreodon beds on Bad Land Creek, Sioux Co., Neb.

The Skull, Plate XV.

The skull is about one fourth smaller than that of *Daphœnus felinus* and is of about the same size as that of *D. hartshornianus*. Seen from above it appears broad and short, with a relatively very large brain-case and broad frontals when compared with Daphœnus or Proamphicyon. Throughout the anterior two thirds of its length the sagittal crest is reduced to a low sharp ridge rising just above the surface of the brain-case, as shown in Pl. XV., Figs. 1 and 2, in marked distinction from the conditions that obtain in this region in the two preceding genera. Posteriorly the sagittal crest is higher and unites with the high and sharp occipital crest which overhangs the occipital condyles. The frontals are broad and bear rather prominent and rugose postorbital processes from which superciliary ridges extend, converge and meet posteriorly at an acute angle to form the low, sharp sagittal crest. There is a marked lateral constriction in the facial region midway between the canine and the infraorbital foramen. The anterior process of the frontals is not so widely separated from the posterior projection of the premaxillaries as in Daphœnus. The nasals are rather broad anteriorly and bluntly pointed posteriorly. The premaxillaries are small and there is a constriction between the canine and I.^{3} for the accommodation of the lower canine.

Seen from the side the top of the skull appears nearly flat longitudinally with the facial region perhaps a little more elongate proportionately than in the preceding genera. The zygomatic arches are very slender and but moderately expanded. Posteriorly they do not expand so abruptly from the margins of the skull as in Daphœnus. The postglenoid processes are directed downward and slightly forward while the paroccipital processes point downward and backward at an angle of about forty-five degrees. The *foramen magnum* is broader than deep, as in modern dogs, although these proportions may have been materially altered by crushing.

Seen from below the palate appears broad and proportionately somewhat longer than in *Daphœnus* and *Proamphicyon*. The anterior palatine foramen is small. The anterior border of the posterior nares is a little posterior to the last molar. The pterygoid plates are continued far back and arch inward in such manner as to partially enclose the narial passage in this region, which in life was doubtless covered over inferiorly by a membrane. The foramen ovale and posterior opening of the alisphenoid canal have a common opening. The foramen rotundum, sphenoidal fissure and optic foramen are present, but the skull is too much crushed in this region to determine their character with certainty. As in Daphœnus the auditory bullæ are not preserved, doubtless through imperfect ossification. The periotic is present and is inflated to accommodate the cochlea. The postglenoid, condylar,

lacerum posterium and medium and other foramina of this region are preserved, though the outlines of some of them, owing to the absence of the auditory bullæ, are not well shown.

The Mandible.—The mandible (Pl. XV., Fig. 1, and Pl. XVI., Fig. 3) has the inferior border remarkably straight, much as in *Daphænus hartshornianus*. The horizontal ramus retains the same depth throughout its entire length. The masseteric fossa is deep. The angular process is pronounced, the extremity is broken away in both rami, but it was apparently pointed and inclined upward and backward. The postero-external border rises almost perpendicularly from the base of the angular process to the condyle instead of inclining strongly backward as in *Daphænus*. There are two mental foramina, of which the anterior lies directly beneath P. $\frac{1}{1}$, and the posterior beneath the middle of P. $\frac{3}{3}$. The position of both is midway between the alveolar and inferior borders. The symphysial area is small and the union was cartilaginous. The inferior dental foramen is situated rather low, near the inferior border of the ramus, and well back toward the base of the condyle. The coronoid process is injured, but enough is preserved to show that it was high and broad, and rose abruptly from the horizontal ramus at an angle of about 90 degrees.

The Dentition.

Superior Dentition.—Plate XV., Fig. 3. In the structure and arrangement of the teeth the present genus more nearly resembles those conditions which obtain in *Temnocyon coryphæus*, as described and figured by Cope (see Tertiary Vertebrata, p. 896, Pl. LXXI.), than any other species of dog known to the present writer. The alignment of the incisors is more oblique and not so nearly at right angles to the longer axis of the skull as in Daphœnus. This character is not so well shown in the figures as it might be. Incisors $\frac{1}{1}$ & $\frac{2}{2}$ are very small, subequal and much compressed. The position of I. $\frac{3}{3}$ is but little posterior to that of I. $\frac{1}{1}$. Compared with $\frac{1}{1}$ & $\frac{2}{2}$ I. $\frac{3}{3}$ is very large with its posterior border placed far behind that of I. $\frac{2}{2}$. Neither of these characters is sufficiently emphasized in Fig. 3, Pl. XV.

The canines are blunt through wear, stout and considerably compressed, but without anterior or posterior cutting edges.

Premolars $\frac{1}{1}$, $\frac{2}{2}$, $\frac{3}{3}$ are stout and well developed and separated from one another and the canine by short diastemata, while P. $\frac{3}{3}$ is nearly in contact with P. $\frac{4}{4}$. P. $\frac{1}{1}$ is fixed by a single root and consists of a simple cone directed obliquely forward and downward. Premolars $\frac{2}{2}$ & $\frac{3}{3}$ are supported by two roots, the heel of the former is not expanded transversely, but that of the latter is much expanded. The crowns of both these teeth consist of a single median cone without anterior or posterior tubercles.

In the sectorial the antero-internal cone is well developed, while the external or principal cone is proportionately a little lower than in *Daphœnus* or *Proamphicyon*. The posterior cutting blade is proportionately high. There is a well-developed basal cingulum on the external and anterior borders of this tooth.

Molar $\frac{1}{1}$ is large and subquadrangular in outline, quite distinct from the same tooth in *Daphœnus hartshornianus*, as will appear from a comparison of the figure of that tooth shown in Pl. XV. with the figures of the same tooth of the last-mentioned species published by Scott in his "Notes on the Canidæ of the White River Oligocene," Fig. A, 2 and Pl. XIX., Fig. 2. The structure and form of this tooth is, in fact, intermediate between that of *D. hartshornianus* and *Temnocyon coryphæus*, though more closely resembling the latter. The external cusps are subequal and situated well within the external border. The internal cusp is separated from the externals by a deep median valley. The intermediate tubercles are faint. The internal basal cingulum is strong and developed into a prominent cone on the postero-internal angle. There is a basal cingulum on the external border of this tooth. M.$^{\frac{2}{}}$ is much smaller but of the same general pattern as M.$^{\frac{1}{}}$ except that the postero-external cone is much smaller than the antero- and occupies a more external position than the latter. M.$^{\frac{3}{}}$ is wanting on either side in the present specimen. But on the left side there is preserved what appears to be a single very small alveolus not shown in the figure. This indicates that this tooth may have been present, but if so, was much reduced in size.

Inferior Dentition. Pl. XVI., Fig. 3.

The incisors are wanting in both rami and hence nothing can be said concerning their character.

The canine is compressed laterally but without anterior or posterior trenchant edges.

The crown of P.$_{\frac{1}{1}}$ consists of a compressed cone, elliptical in cross-section and directed strongly forward. It is fixed in the jaw by one root.

The succeeding premolars are each supported by two fangs and the crowns grow successively stronger from the second to the fourth. They are not reduced in size and separated by but slight diastemata. All bear well-developed basal cingula on their posterior borders, and in addition to the principal median cone there is present on P.$_{\frac{4}{4}}$ a prominent posterior conule.

The inferior sectorial, M.$_{\frac{1}{1}}$ consists of a prominent anterior trigon and a low basal heel. The external cone of the trigon is the strongest and highest, while the postero- and antero-internal cones are smaller and subequal in height and strength.

The structure of the talon has been somewhat obliterated by wear, but it appears to have been composed of a large median cone or ridge homologous with the external cone of the heel in Daphœnus and a rudimentary internal cone.

M. $\frac{2}{2}$ is much reduced in size and its structure has been obliterated by wear to such an extent that it is impossible to determine its exact character.

M. $\frac{3}{3}$ is wanting on both sides, but the single rather small alveolus indicates that it was much reduced in size.

The Vertebræ. Pl. XVIII., Figs. 6, 7, 8.

Of the vertebræ only the atlas, axis, and the third cervical are preserved. These, as in Daphœnus, are feline rather than canine in character. The transverse processes of the atlas are wanting. The articular surfaces for the occipital condyles are deeply concave and rather widely expanded, while those for the axis are nearly flat and but little expanded, diverging from the longitudinal axis at an angle of scarcely more than fifteen degrees. The vertebrarterial canal is somewhat intermediate in character between that of the dogs and cats. It enters on the inferior side at the middle of the base of the transverse process and emerges posteriorly at the supero-posterior border of the base of the same process, instead of directly in the middle, as in Daphœnus and modern cats. The position of the posterior opening of the vertebrarterial canal in the present genus and species while still similar to that which obtains in Daphœnus and the cats is clearly shifting to that which it occupies in the dogs. In this respect Protemnocyon may be considered as having made a distinct advance over Daphœnus in the direction of recent dogs.

The axis is in a splendid state of preservation. The spine is high and sharp, and posteriorly it is continued into a long peg-like process as in the cats instead of being truncated as in the dogs. The odontoid process is peg-like. There are rather slender transverse processes directed backward and slightly downward. Inferiorly there is on the centrum a sharp median keel. Cervical three does not differ materially from the same vertebra in recent cats.

Principal Measurements of Type (552).

Greatest length of skull	167	mm.
" breadth "	85	"
Length of sagittal crest	68	"
Breadth of cranium at greatest temporal constriction	23.5	"
Greatest breadth of cranium	46	"
" " frontals	36	"
Length of palate	81	"
Distance from incisive alveolar border to anterior border of orbit	65	"

Greatest length of lower jaw	116	mm
Depth of lower jaw below $M._{\overline{2}}$	19	"
" " " " $P._{\overline{2}}$	16	"
Height of coronoid process	56	"
Length of sup. premolar-molar series	58	"
" " " series	43	"
" " sectorial	15	"
Breadth " "	9.5	"
" " $M.^1$	15.5	"
" " $"^2$	11	"
Antero-posterior diameter of sup. canine at base of crown	8.5	"
Transverse " " " "	6	"
Length of inferior premolar-molar series	65	"
" " " series	38	"
" " sectorial	16	"
" " $P_{\overline{4}}$	11	"
Breadth " "	5.5	"
Antero-posterior diameter of lower canine	9	"
Transverse " " "	5	"
Expanse of condylar cotyloids of atlas	32	"
Length of centrum of axis including odontoid process	44	"

Relations of Protemnocyon Inflatus.

From the foregoing description and the accompanying figures it will readily appear that the type of the present genus and species very closely resembles Cope's *Daphænus hartshornianus* and there is no doubt that the two are generically identical, though the species are easily distinguishable by the structure of the second inferior molar and of $P.^3$. From several characters already pointed out in the description of both the present and the preceding genus it has appeared to the writer best to subdivide Daphœnus into two genera, viz., *Daphænus* and *Protemnocyon*, including in the latter Cope's species, described as *D. hartshornianus*, which would then be known as *Protemnocyon hartshornianus*.

The present genus appears to stand directly ancestral to *Temnocyon coryphæus* Cope of the John Day. The relationships between the two are shown not only in the dentition, but by certain characters exhibited by the skull and mandible as well. Among the latter may be mentioned *the capacious brain-case, reduced sagittal crest, broad frontals, slender and straight mandible*. *T. coryphæus* has advanced so far beyond *P. inflatus* as to have completely ossified tympanics, which appear as large inflated auditory bullæ. The molars are also much more reduced in the John Day form, the second tubercular having become much smaller than in Protemnocyon of the White River, while the third has disappeared entirely, as might be expected from the exceedingly reduced nature of that tooth in *P. hartshornianus* and *inflatus*, the earlier forms.

CYNODICTIS GREGARIUS Cope.

There are in our collections a number of skulls associated with more or less complete skeletons which I have referred to the above genus and species. With the exception of the os penis which has already been described, these remains throw no new light on the osteology of that genus of Oligocene dogs and hence require no further reference here.

CONCLUSIONS.

The principal object in the preparation of the present paper has been to give to students of the Canidæ, in so far as possible, an accurate description of the osteology of *Daphœnus felinus*, supplemented by good figures based upon the skeleton of a single individual. With the exception of the scapula, pelvis, and certain of the vertebræ and sternals our skeleton, No. 492, is exceptionally complete and thus affords a safe and reliable guide to the osteology of at least one species of Oligocene dogs. After a prolonged and careful comparative study of this skeleton, together with the associated material in our collections, the present writer was forced to the conclusion that among the larger White River Canidæ there are represented three distinct genera two of which had been previously unrecognized, all having been heretofore referred to the single genus *Daphœnus*. Of these three genera two, Daphœnus and Proamphicyon, include species which are larger than those of the third and may be referred to collectively as dolichocephalic or long-skulled, while those belonging to the third genus, *Protemnocyon*, are smaller and brachycephalic or short-skulled.

Briefly these three genera, which in fact represent three distinct phyla, may be characterized as follows:

1. DAPHŒNUS.—*Skull elongate, sagittal crest high, brain-case reduced, canines stout and round without anterior or posterior cutting edges, premolars strong and, save in* D. DODGEI, *with* $M.^{\frac{3}{3}}$ *small and aligned with internal cones of preceding molars, position of vertebrarterial canal in atlas as in the cats. No known descendant.*

2. PROAMPHICYON.—*Skull elongate; sagittal crest high; brain-case reduced; canines long, compressed and with posterior cutting edge; premolars much reduced in size and well spaced;* $M.^{\frac{3}{3}}$ *large with two roots? Ancestral to* AMPHICYON *of the Loup Fork.*

3. PROTEMNOCYON.—*Skull short; sagittal crest low; brain-case large; canines compressed but without cutting edges; premolars strong and rather closely set;* $M.^{\frac{3}{3}}$ *very small or absent; position of vertebrarterial canal of atlas intermediate between dogs and cats; ancestral to Temnocyon of the John Day.*

Concerning the very difficult subject of the relations of the Oligocene canidæ to recent forms, the present writer does not feel competent to enter into a discussion,

especially with the very limited osteological material at his command with which to make the necessary comparisons. From the many feline characters which have been shown to occur in *Daphænus* and other Oligocene dogs and from the many skeletal characters held in common by these dogs and the contemporaneous Machairodonts there would seem but little doubt that both these groups as well as the true felidæ came from a common ancestral stock which most likely belonged to some member of the *Creodonta adaptiva* of Matthew in the early Eocene.

In a paper entitled "The Ancestry of Certain Members of the Canidæ, the Viverridæ and Procyonidæ," published as Article VI. of Vol. XII. of the American Museum Bulletin, Wortman and Matthew have devoted a great deal of attention to the phylogeny of certain genera and species of recent canidæ. With characteristic ingenuity and commendable patience they have developed and proposed two lines of descent, one for the Dholes, and another for those South American foxes with reduced premolars, *Canis urostictus, parvidens*, etc. Considering that these theoretical phylogenies are, for the most part, based on tooth-structure alone, and that throughout vast periods of time we have not yet discovered the intermediate forms which must of necessity have existed, such phylogenetic work while extremely interesting, not to say alluring, must necessarily be quite provisional and theoretic, and it would therefore seem to the present writer a little premature to say that "The Dhole or Red Dog of India (Cyon) can be confidently considered as the living representative of the John Day genus Temnocyon" when not a single intermediate form is known from the close of the Oligocene to recent times. By this I do not mean to deprecate such attempts at working out the ancestry of living animals, which is and should be one of the chief aims of the paleontologist, but rather to emphasize how fragmentary our actual knowledge of the ancestors of the modern canidæ really is. Of the extinct canidæ of North America we are fairly well acquainted with the osteology of but four genera, *Vulpavus* of the Eocene, and *Cynodictis, Daphænus* and *Temnocyon* of the Oligocene.

The plates accompanying this paper were drawn by Mr. F. von Iterson, the text figures by Mr. Sidney Prentice.

Carnegie Museum, July 15, 1902.

Explanation of Plates.

Plate XIV.

Fig. 1. Top view of skull of *Daphœnus felinus* Scott (No. 492). Natural size.
Fig. 2. Side view of same skull. Natural size.

Plate XV.

Fig. 1. Side view of skull of *Protemnocyon inflatus* Hatcher, type (No. 552).
Fig. 2. Top view of same.
Fig. 3. Inferior view of right side of same. All figures natural size.

Plate XVI.

Fig. 1. Inferior view of posterior portion of skull of *Cynodictis gregarius* Cope (No. 493).
Fig. 2. Left ramus of *Daphœnus felinus* Scott (No. 492). Seen from inner side.
Fig. 3. Crown view of right ramus of *Protemnocyon inflatus* Hatcher, type (No. 552).
Fig. 4. Crown view of right ramus of *Daphœnus felinus* Scott (No. 492).
Fig. 5. Inferior view of left side of skull of *Daphœnus felinus* Scott (No. 492). Incisors and $P.^{\frac{1}{1}}$ conjectural, remaining teeth in part restored from No. 553. All figures natural size.

Plate XVII.

Vertebræ of *Daphœnus felinus* Scott (No. 492).
Figs. 1, 2, 3. Inferior, superior, and posterior views of atlas.
Fig. 4. Fifth dorsal, seen from right side.
Fig. 5. Thirteenth dorsal, seen from right side.
Figs. 6, 7. First caudal, seen respectively from right side and above.
Figs. 8, 9, 10, 11, 12. Superior views of fifth, seventh, ninth, thirteenth and twenty-first caudals.
Figs. 13, 14, 15. Lumbars, 2, 4, 7, seen from right side.
All figures natural size.

Plate XVIII.

Fig. 1. Mesosterni 1–5 of *Daphœnus felinus* Scott (No. 492), seen from above
Figs. 2, 3. Os penis of *Cynodictis gregarius* Cope (No. 493), inferior and lateral views.
Figs. 4, 5. Os penis of *Daphœnus felinus* Scott (No. 492), inferior and lateral views.
Fig. 6. Axis of *Protemnocyon inflatus* Hatcher (No. 552), seen from left side.
Fig. 7. Superior view of atlas of same, seen obliquely from behind.
Fig. 8. Left side of third cervical of same.
Fig. 9. Front view of right-hind foot of *Daphœnus felinus* Scott (No. 492).
Fig. 10. Front view of right fore foot of same.
All figures natural size.

PLATE XIX. Limb bones of *Daphœnus felinus* Scott (No. 492).

Fig. 1. Front view of right femur.

Fig. 2. Distal end of same.

Fig. 3. Front view of right tibia.

Fig. 4. Distal end of same.

Figs. 5, 6. Internal and external views of right fibula.

Fig. 7. Posterior view of right humerus.

Figs. 7a, 8. Distal and proximal ends of same.

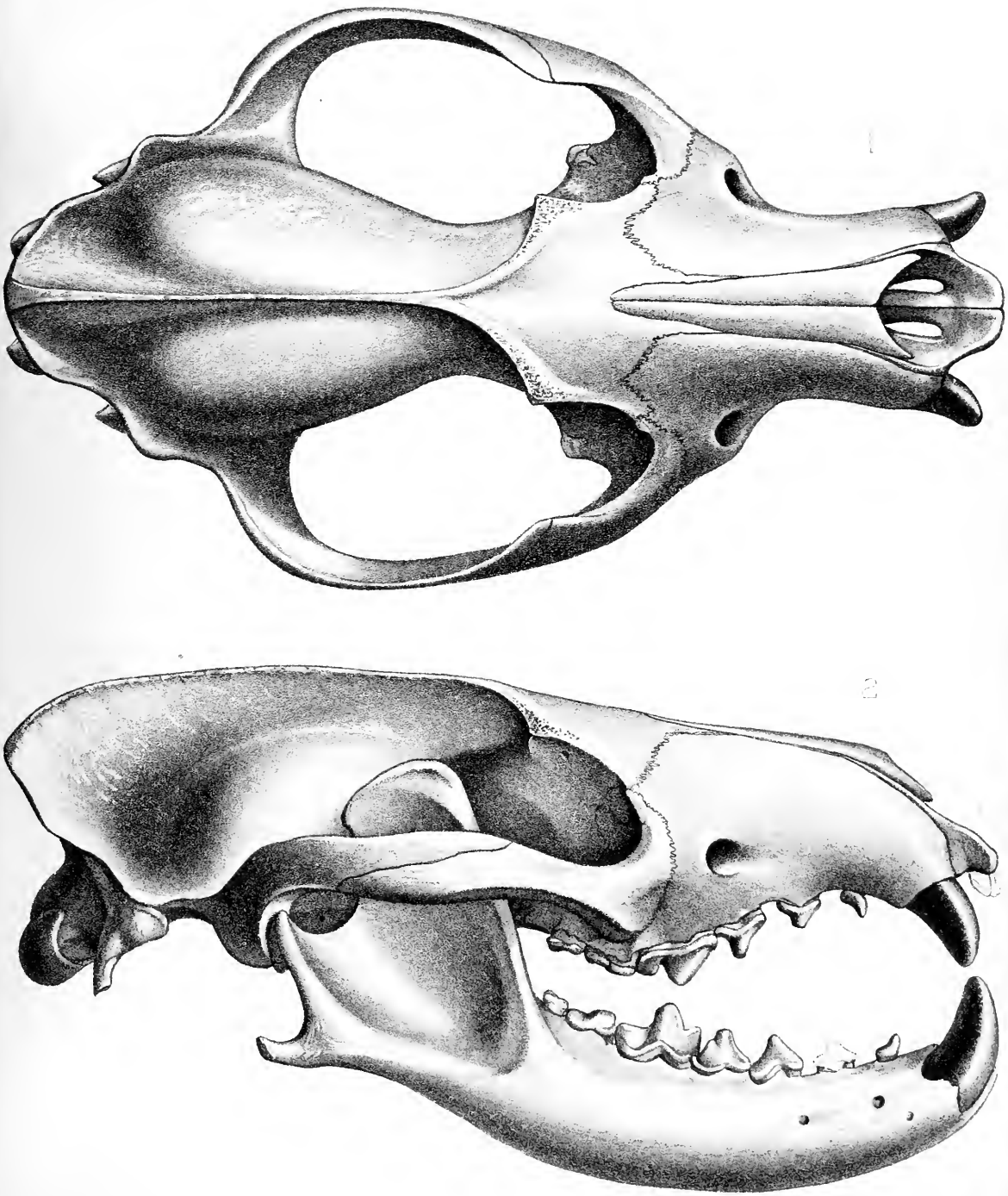
Fig. 9. Posterior view of right radius.

Figs. 10, 11. Proximal and distal ends of same.

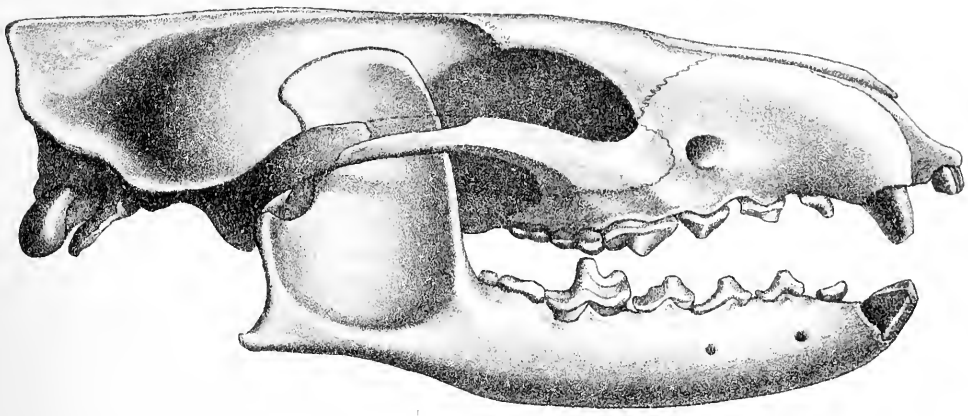
Fig. 12. Front view of right ulna.

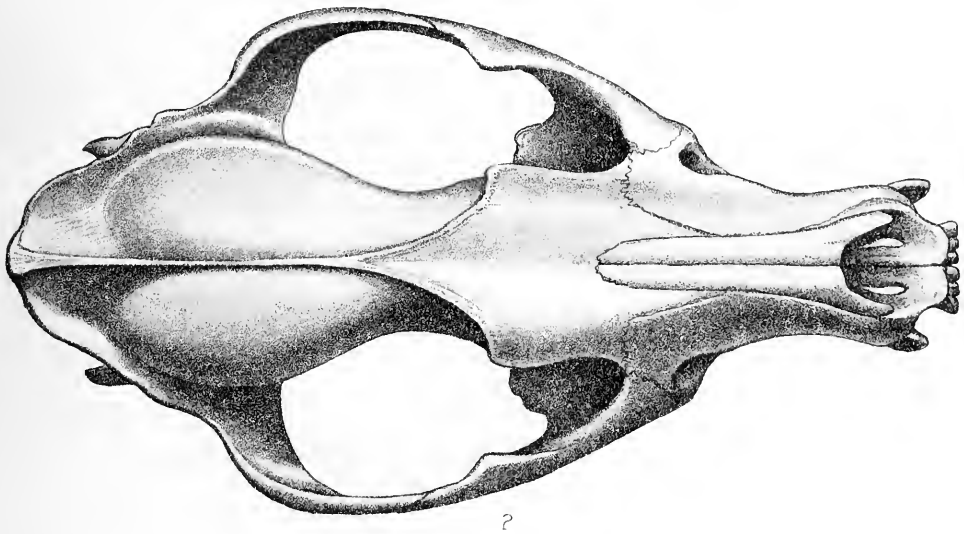
All figures natural size.

PLATE XX. Mounted skeleton of *Daphœnus felinus* Scott (No. 492) $\frac{1}{6}$ natural size.



OLIGOCENE CANIDAE





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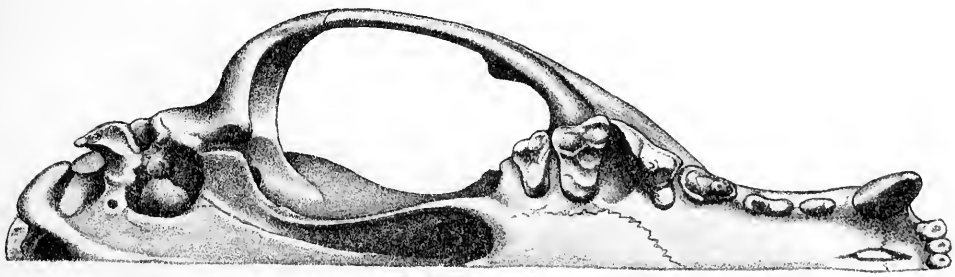

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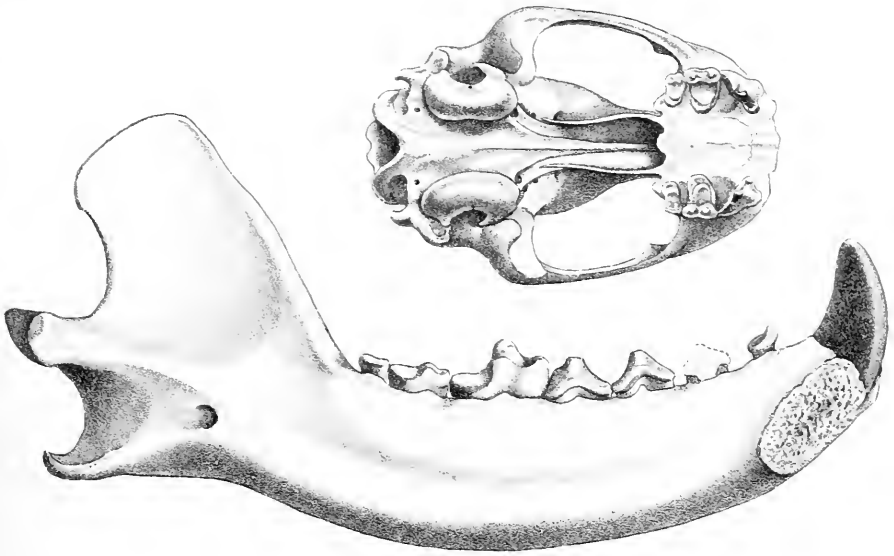

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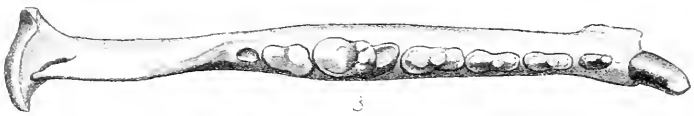

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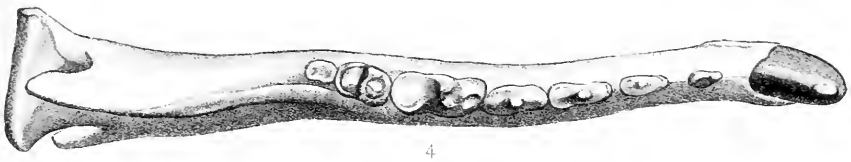

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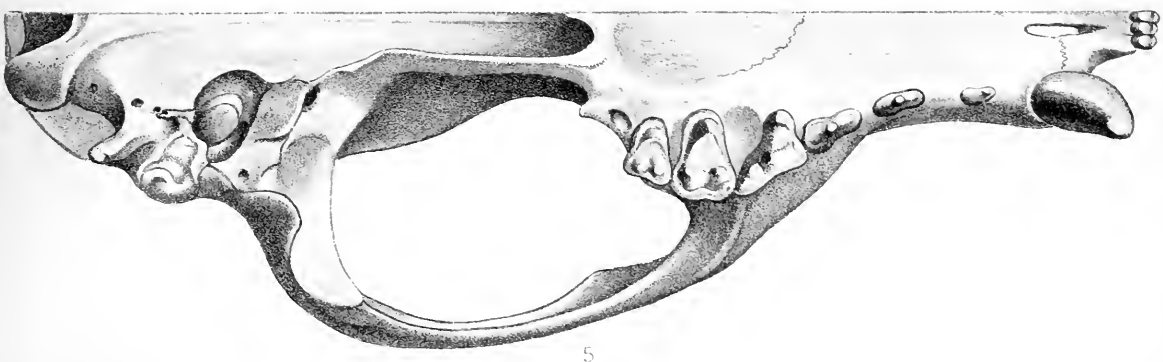

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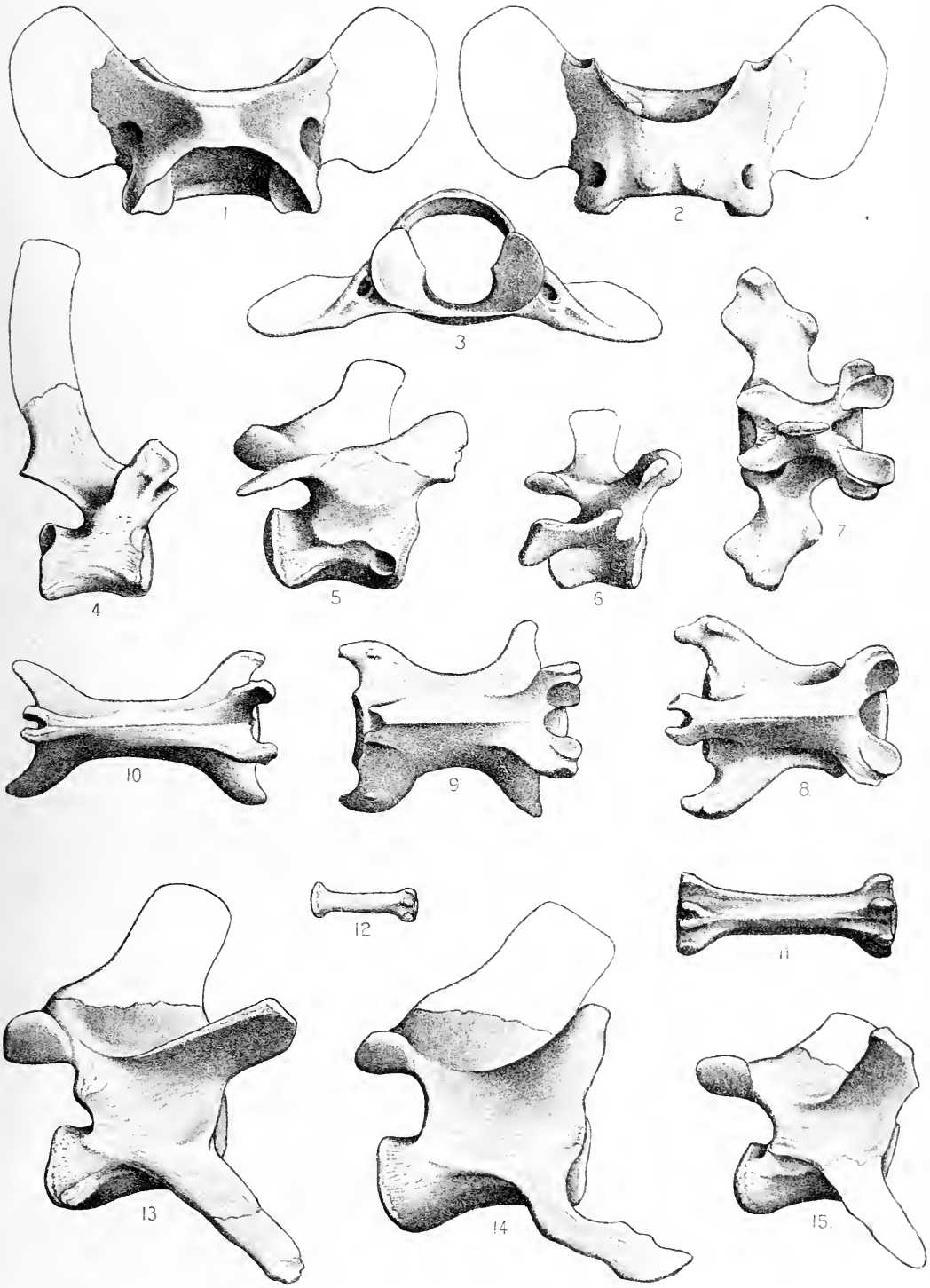
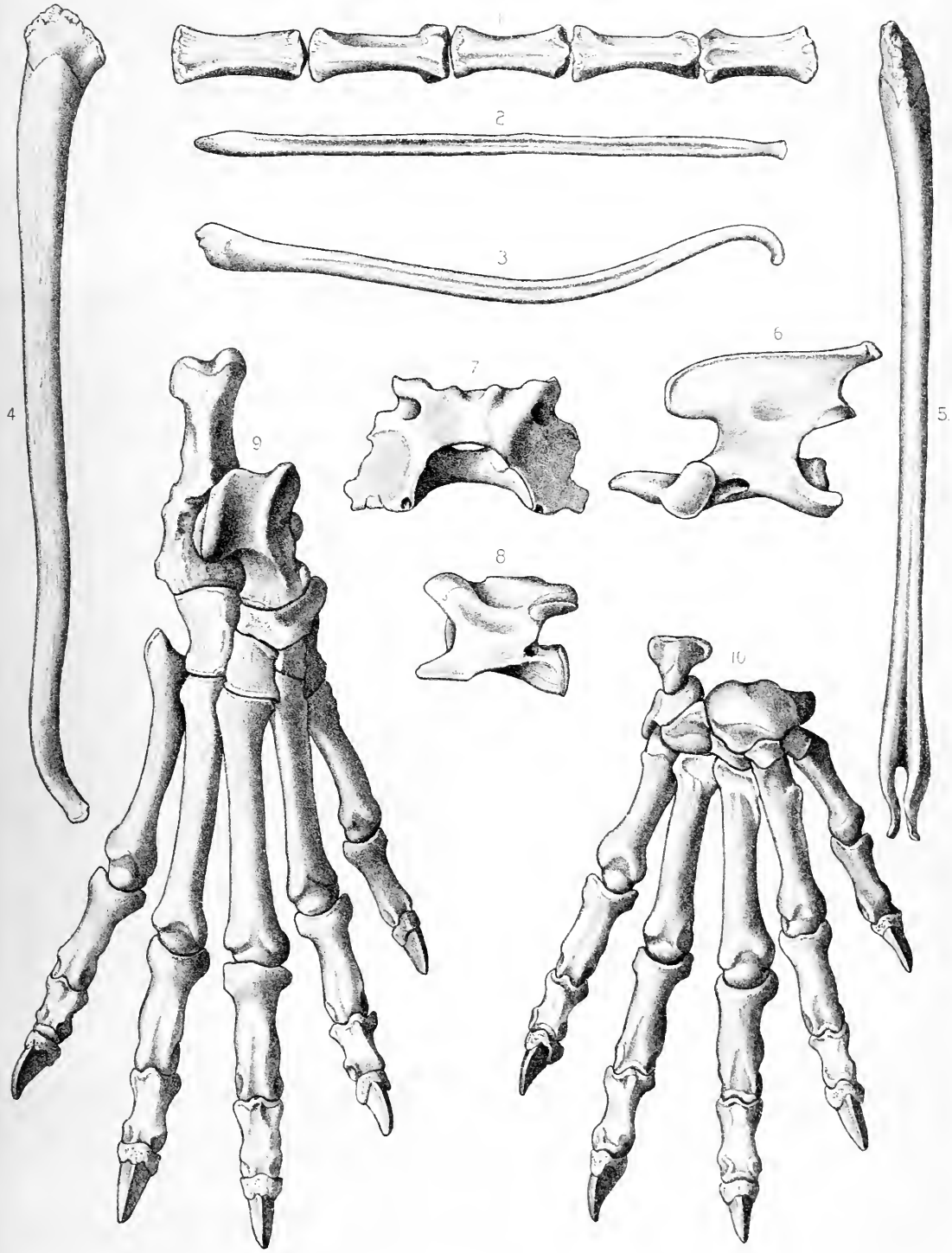
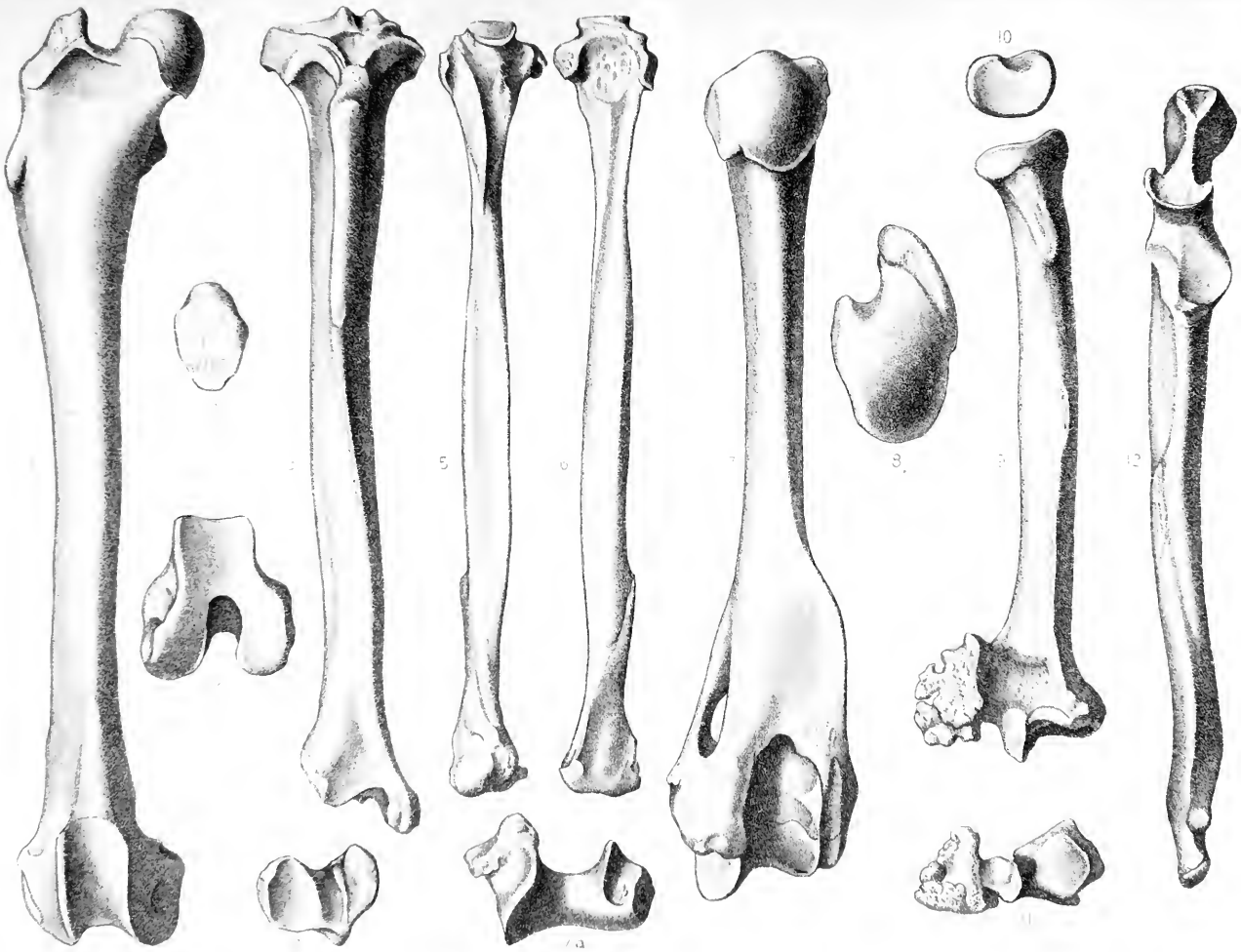


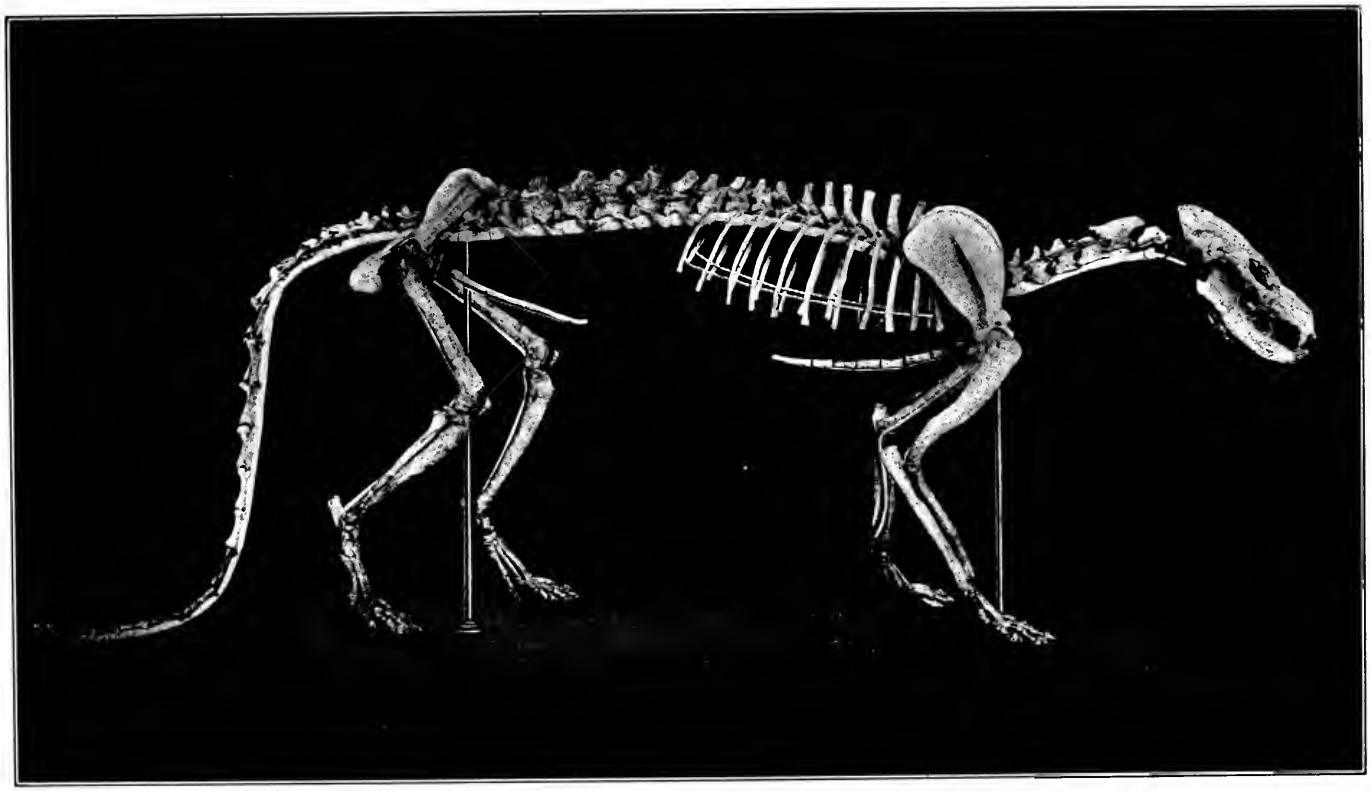
Explanation of plate



OLIGOCENE CANIDAE



OSTEOLOGY OF CAUDAL



SKELETON OF DAPHOENUS FELINUS Scott, ⅛ natural size. Discovered by O. A. Peterson; mounted by Arthur S. Coggeshall. Carnegie Museum, Dept. of Paleontology (No. 492).